CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA
THE AMMONITE FAMILY LYTOCERATIDAE NEUMAYR, 1875

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(With 53 figures)

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ABSTRACT

Ammonites referred to the family Lytoceratidae Neumayr, 1875, occur in rocks of Barremian, Aptian and Albian age in northern Zululand, South Africa, and represent the most southerly Cretaceous records of all the species present. The following are described: *Lytoceras vogdti* Karakasch, which is common in the Aptian, *Lytoceras* aff. *sauclum* (Drushchitza), represented by a single specimen from the Aptian, and *Lytoceras hennigi* Zwierzycki, which is frequent in the Upper Barremian and was previously known only from Tanzania. *Eulytoceras* is represented in the Upper Barremian by the widely occurring *E. phestum* (Matheron); *A.* (*Ammonoceratites*) *mahadeva* (Stoliczka) occurs in the Middle and Upper Albian, and *A.* (*Ammonoceratites*) *crenulatum* (Crick), *A.* (*A.*) *ezoense* (Yabe) and *A.* (*A.*) *crenocostatum* (Whiteaves) are shown to be synonyms of Stoliczka's species. *A.* (*Argonauticeras*) *depereti* (Kilian), of which *A.* (*A.*) *argonautarum* (Anderson) and *A.* (*A.*) *belliseptatum* (Anthula) are considered synonyms, occurs in the Upper Aptian; a form referred to as *A.* (*A.*) aff. *depereti* is present in the Albian, accompanying *A.* (*A.*) *besairiei* Collignon. *Protetragonites* is represented in the Upper Albian by the widely occurring *P. aeolus aeolus* (d'Orbigny).

The genus *Pictetia* is regarded as only a doubtful lytoceratid, perhaps better classed with the Ancyloceratina; it is represented by a specimen referred to as *Pictetia* aff. *depressa* (Pictet & Campiche). A number of important specimens, including the types of *A.* (*Ammonoceratites*) *ezoense*, *A.* (*Am.*) *crenulatum* and *A.* (*Argonauticeras*) *belliseptatum*, are figured photographically for the first time.

CONTENTS

INTRODUCTION

The Lytoceratidae are represented by nine species in the South African Cretaceous, all referrable to the subfamily Lytoceratinae Neumayr, 1875, of

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which the Hemilytoceratinae Spath, 1927, and Protetragonitidae Spath, 1927, are regarded as inseparable parts.

The Lytoceratinae are the rootstock of the Lytoceratina, ranging from Triassic to mid-Cretaceous. They are a morphologically conservative group, with long and widely ranging genera and species. During the late Jurassic and Cretaceous the group were commonest in the Mesogean Realm, although known from as far north as Greenland and as far south as the sub-Antarctic Islands, and typically rare in the Boreal Realm of western Europe and the United States Western Interior.

The following species are described below:

Lytoceras vogdti Karakasch, 1907
Lytoceras aff. *sauclum* (Drushchitza, 1956)
Lytoceras hennigi Zwierzycki, 1914
Eulytoceras phestum (Matheron, 1878)
Ammonoceratites (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865)
Ammonoceratites (*Argonauticeras*) *depereti* (Kilian, 1892)
Ammonoceratites (*Argonauticeras*) aff. *depereti* (Kilian, 1892)
Ammonoceratites (*Argonauticeras*) *besairiei* Collignon, 1949
Protetragonites aeolus aeolus d'Orbigny, 1850
Pictetia aff. *depressa* (Pictet & Campiche, 1861)

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the materials studied:

BMNH	British Museum (Natural History), London
IGS	Geological Museum, London
MNHP	Muséum d'Histoire Naturelle, Paris
SAM	South African Museum, Cape Town
SAS	South African Geological Survey, Pretoria
GSC	Geological Survey of Canada, Ottawa
UPG	University of Pretoria, Geology department

FIELD LOCALITIES

Details of field localities referred to in the paper are given in Kennedy & Klinger (1975).

DIMENSIONS OF SPECIMENS

Dimensions of specimens are given in millimetres; abbreviations are as follows:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter.

Figures in parentheses are dimensions as a percentage of total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916; see Kullman & Wiedmann 1970 for a recent review) is followed in the present work:

I_s = Internal lobe with septal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

SYSTEMATIC PALAEONTOLOGY

Phylum **MOLLUSCA**
Class CEPHALOPODA Cuvier, 1797
Subclass AMMONOIDEA Zittel, 1884
Order LYTOCERATIDA Hyatt, 1899
Superfamily LYTOCERATACEAE Neumayr, 1875
Family **LYTOCERATIDAE** Neumayr, 1875
Subfamily Lytoceratinae Neumayr, 1875

Genus *Lytoceras* Suess, 1865

Types species

Ammonites fimbriatus J. Sowerby, 1817 (I.C.Z.N. Opinion 130).

Diagnosis

Evolute, serpenticone, whorls slowly expanding, with a rounded to quadrate whorl section. The surface of the shell is ornamented by fine crenulate ribs or growth lines, and there are periodic flares, each associated with a constriction on the internal mould. The shell surface may be finely striate. Suture formula ELU_2 (U_{1v} : U_{1d}) I_s; highly subdivided, with a short external lobe (E) and a triangular, highly subdivided lateral (L) lobe. There is a large septal lobe.

Discussion

Lytoceras is a conservative genus, ranging through the Jurassic and Lower Cretaceous with very little change. There have been repeated attempts to subdivide the genus, but the authors follow Arkell & Wright (1957), Wiedmann & Dieni (1968) and others in regarding *Ophiceras* Suess, 1865, *Fimbrilytoceras* Buckman, 1918, *Thysanoceras* Hyatt, 1867, *Thysanolytoceras* Buckman, 1905, *Kallilytoceras* Buckman, 1921, *Crenilytoceras* Buckman, 1926, *Orcholytoceras* Buckman, 1926, *Biasaloceras* Drushchitza, 1953, *Valentolytoceras* Beznosov, 1958, and *Dinolytoceras* Beznosov, 1958, as synonyms.

Hemilytoceras Spath, 1927 (type species *Ammonites immanis* Oppel, 1865), has rounded and smooth inner whorls, and on the outer whorl develops high, concave, closely spaced lamellar flares. *Metalytoceras* Spath, 1927 (type species *Lytoceras triboleti* Hohenegger *in* Uhlig 1883), is a compressed, finely ribbed genus, with very weak constrictions, and is readily separable from *Lytoceras* by virtue of the consistent splitting of the ribs into fine riblets over the venter. *Pterolytoceras* Spath, 1927 (type species *Ammonites exoticus* Oppel, 1865), is very loosely coiled, with slowly expanding subcircular whorls; the ornament is

much finer than in *Lytoceras*, and rather irregular.

Eulytoceras Spath, 1927 (type species *Ammonites inaequalicostatus* d'Orbigny, 1840), differs from *Lytoceras* in having regular, distant ribs and periodic flares, with fine striae or riblets between. In the type species, this ornament survives in adults, as it does in *E. phestum* (Matheron). There are, however, species such as '*Biasaloceras*' *sauclum* Drushchitza which have *Eulytoceras*-like inner whorls, but develop a *Lytoceras*-like adult ornament of fine, crinkled ribs and flares with associated constrictions. These forms are both classed with *Lytoceras sensu stricto* here, but they point to the homogeneity of the Lytoceratinae and the problem of placing many 'intermediate' species within the group.

The remaining Cretaceous Lytoceratinae are readily distinguished from *Lytoceras*; in *Pictetia* Uhlig, 1883 (type species *Crioceras astierianum* d'Orbigny, 1842), the whorls are not in contact, whilst there are no flares or constrictions. These are also generally absent in the rapidly expanding, finely ribbed *Ammonoceratites* (*Ammonoceratites*) and *A.* (*Argonauticeras*), although, as is noted later, the dividing line between many lytoceratid genera discussed here is sometimes exceedingly thin.

Occurrence

Lytoceras ranges from the Lower Jurassic (Pliensbachian) to the Cenomanian, with a world-wide distribution extending as far north as Japan, Greenland and Alaska, and as far south as Zululand and the sub-Antarctic Islands. In the Cretaceous, the group is unknown in the Boreal region of northern Europe and the Western Interior of North America.

Lytoceras vogdti Karakasch, 1907

Figs 1–8, 9A, 12A, F–G

Lytoceras vogdti Karakasch, 1907: 51, pl. 5 (fig. 1), pl. 24 (fig. 31), pl 26 (fig. 7). Förster, 1975: 143, pl. 1 (fig. 3).

Pictetia vogdti Drushchitza, 1956: 82, pl. 5 (fig. 19), text-fig. 36a–d. Drushchitza & Kudryavtseva, 1960: 257, pl. 6 (fig. 1a–b), text-fig. 65.

'*Pictetia*' *vogdti* Schindewolf, 1961: 679.

Type

The larger of the two specimens figured by Karakasch (1907, pl. 5 (fig. 1)) is herein designated lectotype of this species; it is from the Barremian of the Crimea.

Material

Large lytoceratids referred to this species are common in the Upper Aptian of Zululand, especially along Mlambongwenya Spruit and in the Mkuze Game Reserve; SAS L/Li, Z1113–4, Z805, 805a and A1158, are all from the Makatini Formation, Aptian IV, at locality 151 in the Mkuze Game Reserve. SAS Z7 (Haughton Collection) is from the Makatini Formation at Haughton's (1936)

Fig. 1. *Lytoceras vogdti* Karakasch, 1907. SAS Z1731. × 0,38.

locality Z7. UPG B391–393 and BMNH C78716 are from the Makatini Formation at locality 171; BMNH C78712, C78715, and C78717 are from the same formation, Aptian IV, at locality 172, Mlambongwenya Spruit. SAS LJE71, BMNH C78702, and possibly C78710 are from the Makatini Formation, Aptian III–IV, at locality 168, Mfongozi Spruit; and BMNH C78703 is from the same horizon at locality 34 on a tributary of the Mzinene River near Hluhluwe, Zululand.

Fig. 2. *Lytoceras vogdti* Karakasch, 1907. SAS Z1731. × 0,38.

Fig. 3. *Lytoceras vogdti* Karakasch, 1907. SAS LJE 71. × 0,38.

Fig. 4. *Lytoceras vogdti* Karakasch, 1907. SAS LJE 71. × 0,38.

Fig. 5. *Lytoceras vogdti* Karakasch, 1907. A. SAS Z1731, showing septal lobe. × 0,45. B. SAS 2805, showing relationship between septal lobe and cruciform internal lobe. × 1,3.

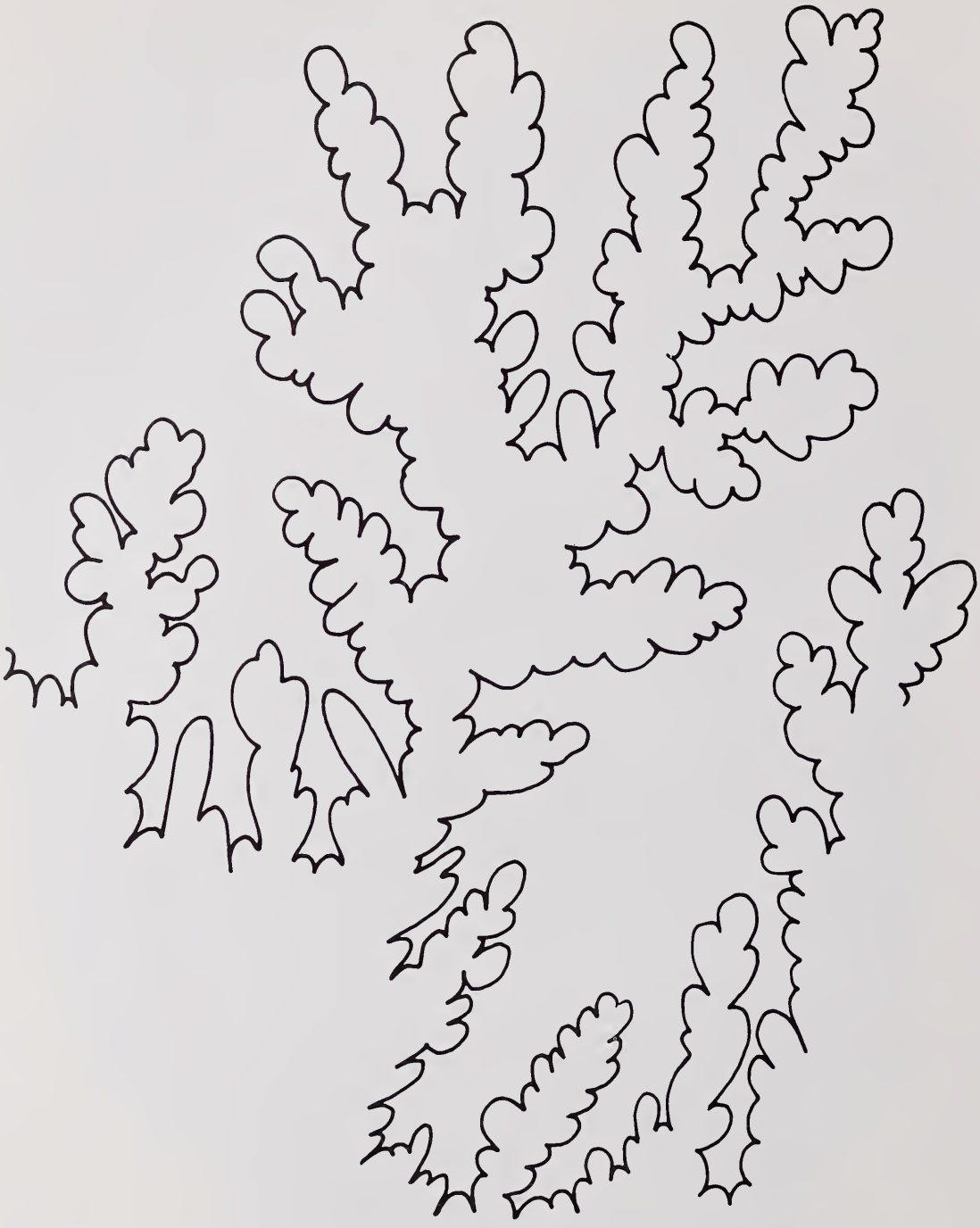

Fig. 6. External suture of *Lytoceras vogdti* Karakasch, 1907. × 4,5.

Fig. 7. *Lytoceras vogdti* Karakasch, 1907. BMNH C78703. × 1.

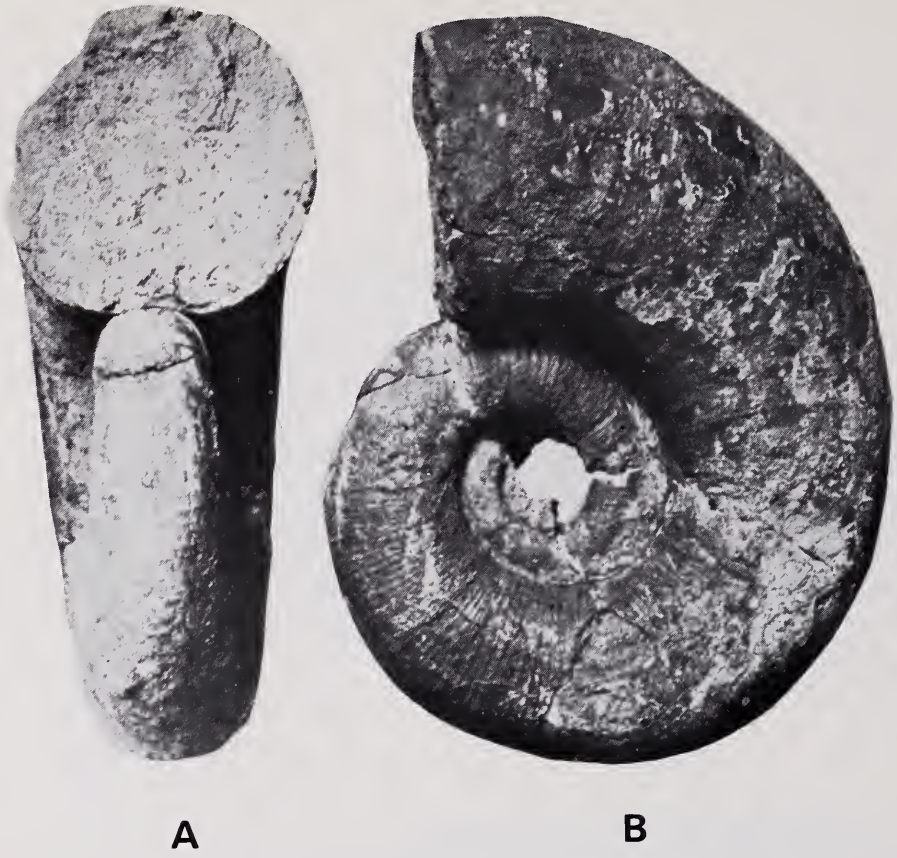

Fig. 8. *Lytoceras vogdti* Karakasch, 1907. Copy of the original figures of the lectotype. × 1.

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
Lectotype (after Karakasch) . .	85,0	34,0(40)	32,0(38)	1,06	30,0(35)
SAS L/Li . . .	155,0	67,5(44)	67,0(43)	1,00	55,0(35)
SAS Z805 . . .	—	82,0(—)	81,0(—)	1,01	— (—)
SAS Z805a . . .	—	76,0(—)	76,0(—)	1,00	
UPG B393 . . .	208,0	95,0(45)	94,0(45)	1,00	— (—)
LJE 71	282,0	130,0(46)	135,0(48)	0,96	80,0(28)
SAS Z113 . . .	330,0	149,0(45)	142,0(43)	1,05	— (—)
UPG B391 . . .	350,0	165,0(47)	161,0(46)	1,02	115,0(33)
SAS Z1114 . . .	405,0	198,0(49)	170,0(42)	1,16	120,0(30)
SAS A1158 . . .	—	211,0(—)	200,0(—)	1,05	— (—)

Description

This is a very large lytoceratid; the largest fragment is still septate at a whorl breadth of 211 mm, corresponding to an estimated total diameter of close on 450 mm for the phragmocone alone. Almost all specimens have very poorly preserved inner whorls, commonly encrusted with oysters, and it has proved impossible to dissect out the nuclei of the giant specimens to confirm that they indeed correspond to the few associated juveniles, the best preserved of which is illustrated as Figures 7A–C, 12A. This individual is partially exfoliated and does not preserve the outer shell surface; it shows, however, very evolute coiling with a shallow dorsal impressed zone, a wide umbilicus and rapidly expanding depressed whorls (Fig. 7A). The exfoliated ornament (Fig. 7B–C) consists of prominent, narrow, fairly distant ribs separated by from three to four fine growth striae. Both ribs and growth striae arise at the umbilical seam; they are concave on the umbilical wall, sweep forwards across the shoulder and are markedly prorsiradiate on the flank, crossing the venter with a broad shallow convexity (Fig. 7B). The specimen bears a single broad constriction, parallel to ribs and striae.

BMNH C78710 (Fig. 12F–G), a fragment tentatively referred to this species, shows perfectly preserved ornament at a whorl height of 42,5 mm. The ribs and striae are markedly prorsiradiate and pass across the venter with but a shallow convexity. Ribs are distant, and minutely crenulated, whilst between them are from three to five growth striae of variable strength and development. In addition, there is a delicate spiral ornament connecting the crinkles on successive ribs.

Beyond 150 mm diameter, it is convenient to describe the specimens in terms of two morphological extremes, with passage forms between. In variety α the dorsum is flattened and the venter quite narrowly rounded. The ribs flex slightly backwards over the umbilical wall and are radial to feebly prorsiradiate on the flanks, crossing the venter with only slight curvature. There are sparse, broad, shallow constrictions bounded by a prominent flared adoral rib. As diameter increases, the ribs become widely spaced and in most specimens growth striae are not preserved although a few specimens (e.g. Fig. 9A) show that both they and the delicate spiral ornament survive. On moulds the ribs appear as low, rounded undulations. In variety β, the venter and dorsum are equally rounded, and the greatest breadth is at mid-flank—a square cross-section in which the corners are rounded. Ribs are distinctly prorsiradiate and there are occasional flared ribs, not, apparently, accompanied by constrictions.

The suture line of this species is deeply and intricately subdivided (Fig. 6); L is large and asymmetrically bifid, U_2 larger than U_1, and I cruciform (Fig. 5B). The septal lobe is massive (Fig. 5A).

Discussion

The lectotype of *Lytoceras vogdti* is a juvenile, but shows an expansion rate and differentiation of ornament into ribs and striae like that of some of the

present similarly sized fragments, sufficient to suggest them to be conspecific. Some of the specimens resemble *Lytoceras mikadyense* Krenkel (1910: 233, pl. 22 (fig. 5)), but this species has consistently wider spaced ribs with striae between, indicating it to be closer to *Eulytoceras*. Of other species described by Krenkel, the unique holotype of '*Crioceras*' *schlosseri* Krenkel (1910: 227, pl. 22(3) (fig. 15)), although more compressed, has ornament like that of some of the present specimens.

Of species described from approximately contemporaneous strata in Madagascar, *Lytoceras* aff. *vicinum* Douvillé of Collignon (1962*b*: 5, pl. 217 (fig. 952)) has a compressed whorl section with delicate concave, prorsiradiate flank ribs, whilst *Lytoceras belliseptatiforme* Collignon (1962*b*: 6, pl. 217 (fig. 953), pl. 218 (fig. 953)) is densely and evenly ornamented by fine ribs, has a lower expansion rate and circular whorl section. *Lytoceras mahafalense* Collignon (1963: 14, pl. 246 (fig. 1503)) has a distinctly compressed oval whorl section and is of Albian age. The most similar species appears to be *Lytoceras* (*Thysanolytoceras*) *strambergense* mut. *albensis* Collignon (1963: 9, pl. 244 (fig. 1047)), a Lower Albian form with rather finer ribbing and a distinctively compressed whorl section and lower expansion rate. The species may be a descendant of the present form.

Occurrence

Lytoceras vogdti was first described from the Barremian of the Crimea; it has been subsequently recorded from the Upper Aptian of Mozambique, and now Zululand.

Lytoceras aff. *sauclum* (Drushchitza, 1956)

Figs 9B, 10A–D, 11B

Compare:

Biasaloceras sauclum Drushchitza, 1956: 71, pl. 4 (fig. 13); Drushchitza & Kudryavtseva 1960: 256, pl. 5 (fig. 1).

Lytoceras sauclum Wiedmann and Dieni, 1968: 29.

Type

The holotype is Drushchitza's (1956, pl. 4 (fig. 13)) original specimen from the Hauterivian of the Crimea.

Material

BMNH C78704 from the Makatini Formation, Albian IV, locality 171, Mlambongwenya Spruit, Zululand.

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
BMNH C78704 .	122,0	52,5(43)	48,0(39)	1,1	49,0(40)

Fig. 9. A. *Lytoceras vogdti* Karakasch, 1907. BMNH C78702, whorl fragment showing details of ornament. × 1. B. *Lytoceras* aff. *sauclum* (Druschchitza, 1956). BMNH C78704, nucleus, showing details of juvenile ornament. × 2.

Description

The coiling is very evolute, serpenticone, with a narrow, shallow, impressed dorsal area. The whorl section is depressed (whorl breadth to height ratio may be up to 1,1), expanding quite rapidly, with the greatest breadth some way below mid-flank. The umbilical seam is deeply incised, the umbilicus of moderate width (about 40% of diameter) and depth. The umbilical wall is high and rounded, the umbilical shoulder broadly rounded, the flanks flattened, ventrolateral shoulders broadly rounded, and the venter somewhat flattened.

The shell is ornamented by growth striae, and widely spaced crinkled ribs. Ribs and striae arise at the umbilical seam, curve backwards across the umbilical wall and forwards across the umbilical shoulder and are straight and slightly prorsiradiate across the flanks. The inner whorls have a distinctive *Eulytoceras*-like appearance, with between seven and ten striae between each pair of ribs, the ribs themselves being distinctly—if minutely—crenulate, with a gently inclined apical slope and an abrupt apertural face which give the surface of the shell a scale-like appearance (Fig. 9B). As size increases (Fig. 10) the ribs become more closely spaced, striae lose their prominence, crenulations become more distinct, and on some specimens, fine strigations appear on some areas of shell. All specimens bear occasional broad, deep constrictions on both shell and mould, preceded by a high, flared rib. Both flares and constrictions become increasingly prominent as diameter increases.

The suture line (Fig. 11B) includes a deeply incised elongate E with a long, narrow lanceolate median saddle, a large, triangular, asymmetrically bifid L, and a similar smaller U_2 lobe, separated by a large, splayed bifid L/U_2 saddle.

Discussion

Drushchitza figured the type specimen of *Biasaloceras sauclum* in side view only, but the illustration shows clearly the differentiation of ornament on the *Eulytoceras*-like early whorls into ribs with groups of striae between, an intermediate stage with rather irregular ornament, and middle to late growth stages with straight, variably spaced crenulate ribs and occasional flares. The whorl section is slightly depressed, with the greatest breadth some way below mid-flank. Although of Hauterivian age, the striking similarity between the illustration and the present material suggests that they belong to the same group, in spite of age difference.

Biasaloceras striatum Drushchitza (1956: 78, pl. 4 (figs 14a–b); Drushchitza & Kudryavtseva 1960, pl. 4 (figs 5a–b)) has a similar juvenile ornament, but a rather different whorl section; based on a juvenile, the authors are inclined to regard it as a possible variant of *L. sauclum*. The markedly different early and late ornament of *Lytoceras sauclum* helps to differentiate it from most Cretaceous *Lytoceras* species. Thus, of the long-ranging Stramberg species, *Lytoceras liebigi* Oppel (Zittel, 1868: 74, pl. 9 (figs 5a–b, 7a–b), pl. 10) has a depressed oval whorl with concave crenulate ribs. *Lytoceras strambergense* Zittel (1868:

Fig. 10. *Lytoceras* aff. *sauclum* (Drushchitza, 1956). BMNH C78704. × 1.

74, pl. 11 (figs 1–3)) has flexuous crenulate ribs, and *Lytoceras sutile* Oppel (1865: 551; Zittel 1868: 76, pl. 12 (figs 1–5)) has a circular whorl section and flexuous ribbing throughout ontogeny. *Lytoceras* aff. *strambergense* of Collignon (1949*a*: 71, pl. 12 (fig. 1), text-fig. 5) from the Hauterivian of Madagascar has distinctly concave ribs and flares. *Lytoceras mahafalense* Collignon (1963: 14, pl. 246 (fig. 1053)) from the Albian of Madagascar has a distinctly compressed whorl section and flattened flanks, whilst *Lytoceras vicinum* Douvillé (1916: 93, pl. 11 (fig. 6)) is also a compressed species with an elliptical to oval whorl section. A final species to mention, *Lytoceras hennigi* Zwierzycki, described below, has a depressed oval whorl section, and a very even, regular ornament.

Occurrence

Lytoceras sauclum was originally described from the Hauterivian of the Crimea and is also recorded from the Valanginian of Sardinia.

Lytoceras hennigi Zwierzycki, 1914

Figs 11A, 12B–E, 13A–E

Lytoceras sp. Krenkel, 1910: 224, pl. 22 (fig. 10).
Lytoceras hennigi Zwierzycki, 1914: 40, pl. 4 (figs 6–7). Spath, 1939: 7.

Type

Lectotype herein designated is Zwierzycki's (1914, pl. 4 (figs 6–7)) original figured specimen from the *Trigonia schwartzi* Bed (Barremian–Aptian) of Mikadi, Tanzania.

Material

Fragments of five individuals and one fairly complete specimen, BMNH C78705–9, C78711, from the Makatini Formation, Barremian 1, locality 171, Mlambongwenya Spruit, northern Zululand.

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
Lectotype (from Zwierzycki) . .	155,0	58,0(37)	57,0(37)	1,02	61,0(39)
BMNH C78708 .	—	37,0(—)	31,0(—)	1,19	—
BMNH C78705 .	—	35,0( )	31,8( )	1,10	—

Description

The coiling is very evolute, with a narrow, shallow impressed area, the whorls expanding quite rapidly. The whorl section is a depressed oval, the greatest breadth being at mid-flank. Ornament consists of fine ribs, growth striae, and occasional flares. These arise at the umbilical seam, sweep sharply backwards over the inner umbilical wall where they are concave, then forwards

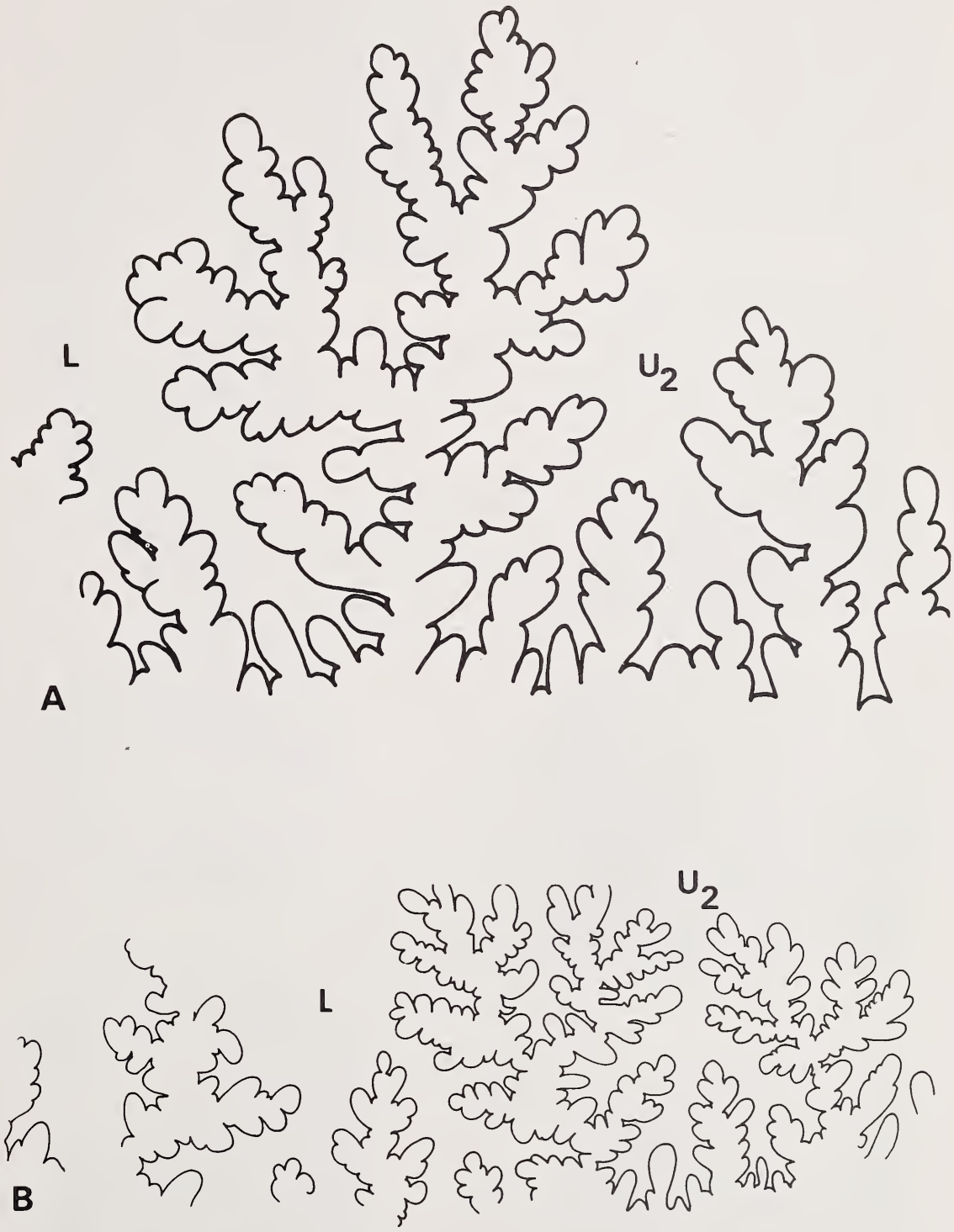

Fig. 11. A. Partial suture of *Lytoceras hennigi* Zwierzycki, 1914. BMNH C78705. × 5. B. Partial suture of *Lytoceras* aff. *sauclum* (Drushchitza, 1956). BMNH C78704. × 4,5.

to pass straight across the umbilical shoulder and flanks where they are markedly prorsiradiate, to cross the venter with a faint forwards projection. The best preserved specimens show the ribs to have been even, sharp-topped and minutely crinkled, and separated by wider interspaces ornamented by irregular fine striae. Delicate spiral ridges connecting crinkles are present over the whole of the shell surface when well preserved. There are periodic high, sharp flares (Fig. 12D–E), although these are only rarely preserved. When shells are partially exfoliated, growth striae, crinkles and strigations disappear, leaving only evenly spaced, rounded ribs and occasional constrictions (corresponding to the site of flares). Moulds are smooth save for constrictions (Fig. 12D).

The sutures are poorly exposed, but include a large E/L and smaller L/U_2, both deeply incised, asymmetric and triangular, separated by a deep splayed L (Fig. 11A). A distinct siphonal band is present in one specimen (Fig. 12D).

Discussion

The present specimens are much smaller than Zwierzycki's lectotype, but a comparison with topotype specimens in the British Museum (Natural History) suggests that they are indeed referrable to *Lytoceras hennigi*. The whorl section of topotype specimens is depressed at small diameters, whilst the ornament consists of even, crinkled ribs with smooth, somewhat wider interspaces between, and occasional strong periodic flares, marked by broad constrictions on the internal mould.

The regular, fine ribs and periodic flares of *L. hennigi* readily distinguish it from *Eulytoceras* species discussed below, whilst *Lytoceras liebigi*, *L. strambergense* and *L. sutile* differ in proportions and ornament, as noted above. *Lytoceras subsequens* Karakash (1907: 49, pl. 5 (fig. 9, 9a), pl. 24 (fig. 32)) lacks prominent constrictions and flares; *L.* aff. *sauclum* has completely different, *Eulytoceras*-like juvenile ornament as discussed above, whilst *Lytoceras puezanus* Haug (1889: 197, pl. 8 (fig. 1) pl. 10 (fig. 1)) has less marked flares and very strong strigations. *Lytoceras densefimbriatum* Uhlig (1883: 191, pl. 6 (figs 1a–c, 2)) is a very finely ornamented, compressed form with weaker flares and stronger strigations, *Lytoceras mahafalense* Collignon is compressed, whilst *Lytoceras subfimbriatum* d'Orbigny (1840: 121, pl. 35) has a compressed whorl section, very fine fimbriate ornament, and distant flares, four to five per whorl.

Occurrence

Lytoceras hennigi is known from the Lower Cretaceous of Tanzania and the Upper Barremian of Zululand only.

Genus *Eulytoceras* Spath, 1927

Type species

Ammonites inaequalicostatus d'Orbigny 1840.

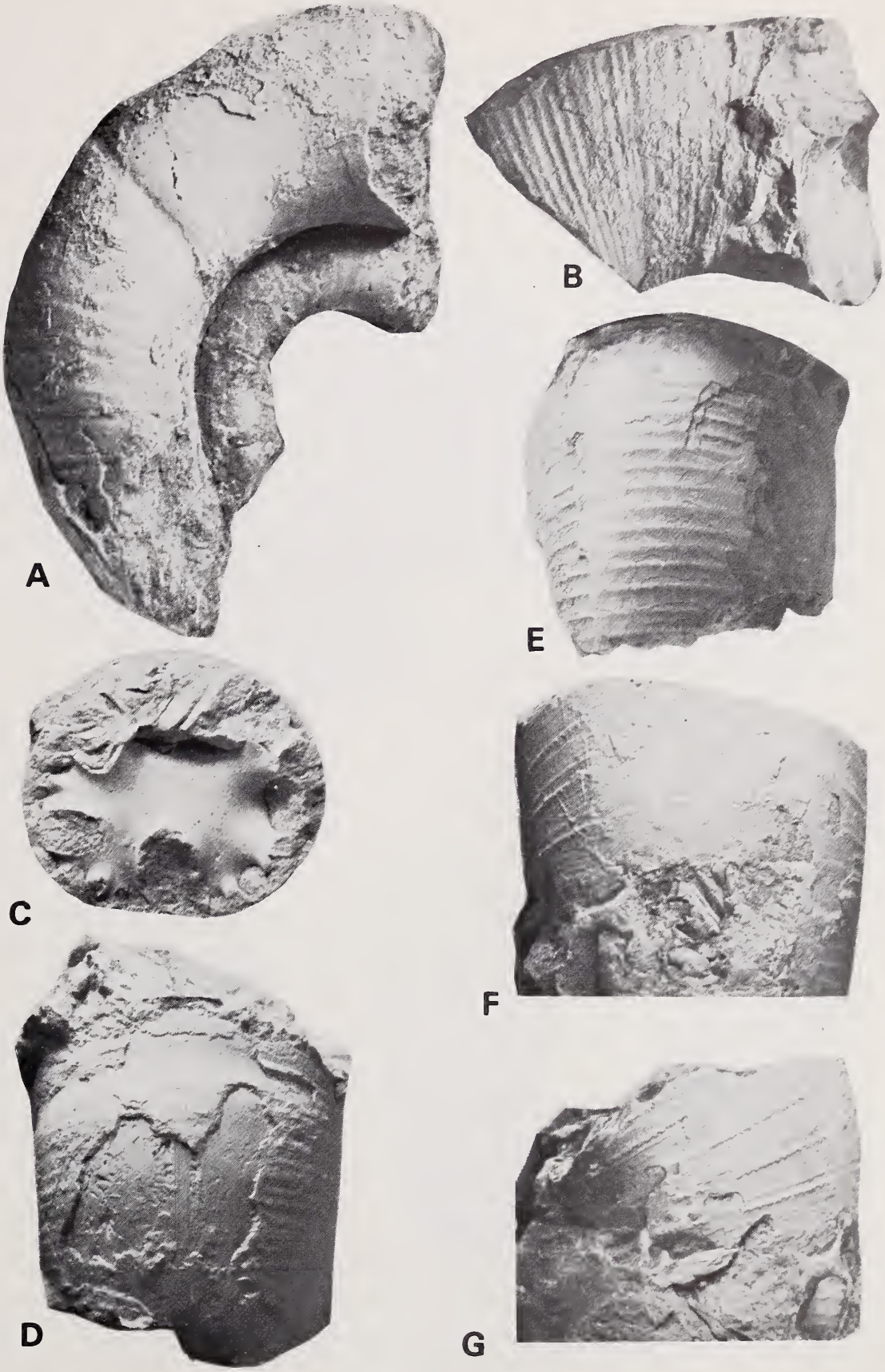

Fig. 12, A, F, G. *Lytoceras vogdti* Karakasch, 1907. A. BMNH C78703. F–G. BMNH C78710. × 1. B–E, *Lytoceras hennigi* Zwierzycki, 1914. B–D. BMNH C78708. E. BMNH C78705. × 1.

Fig. 13. *Lytoceras hennigi* Zwierzycki, 1914. A–B. BMNH C78705. C–E. BMNH C78706. × 1.

Diagnosis

Compressed to round-whorled serpenticone lytoceratids with slowly expanding whorls ornamented by fine, regular, distant rectiradiate to prorsiradiate ribs and periodic flares, all of which extend across the venter without interruption.

Discussion

The regular, fine, distant ribs and occasional simple flares of typical *Eulytoceras* clearly separate them from *Lytoceras* itself (with typically crinkled ribs and flares and periodic constrictions), *Hemilytoceras* (with smooth inner whorls and high, closely spaced concave flares), *Pterolytoceras* (with minutely crinkled growth lines and irregular fine ribs), *Ammonoceratites* (*Ammonoceratites*) and *A.* (*Argonauticeras*), both of which have fine, dense, subdued ornament.

As the authors have noted, however, some species such as *Lytoceras sauclum*, described above, have *Eulytoceras*-like inner whorls, whilst '*Lytoceras*' *mikadyense* Krenkel has *Eulytoceras* inner whorls and develops very closely spaced ornament when adult, being transitional to *Lytoceras sensu stricto*.

Occurrence

Eulytoceras ranges from the Hauterivian to Lower Aptian, and species are known from southern Europe, the Crimea, Caucasus, Bulgaria, east Africa (Tanzania), South Africa (Zululand), Madagascar, and California.

Eulytoceras phestum (Matheron, 1878)

Figs 14A–E, 15

Ammonites phestus Matheron, 1878, pl. c–20 (fig. 5).

Lytoceras phestus Uhlig, 1883: 187, pl. 5 (figs 1–4, 20). Trautschold, 1886: 137. Haug, 1889: 196, pl. 8 (fig. 2). Simionescu, 1898: 59, pl. 2 (figs 4, 10), pl. 20 (fig. 17). Sarasin & Schöndelmayer, 1901: 19. Karakasch, 1907: 46, pl. 4 (fig. 10), pl. 20 (figs 5–6). Pervinquière, 1907: 64. Kilian & Reboul, 1915: 21, pl. 1 (figs 1–2). Petković, 1921: 48. Kulzhinskaya-Voronets, 1933: 5, fig. 6. Rouchadzé, 1933: 174. Ksiażkiewicz, 1938: 230, pl. 1 (fig. 1). Eristavi, 1955: 53; 1957: 59.

Lytoceras gresslyi Somogyi (*non* Hantken), 1914, pl. 11 (fig. 12).

? *Lytoceras lorentheyi* Somogyi, 1914: 300, pl. 11 (figs 10–11).

? *Protetragonites phestus* Nagy, 1967: 62, pl. 2 (fig. 1).

Eulytoceras phestum Spath, 1927: 64. Drushchitza, 1956: 87, pl. 5 (fig. 18); Drushchitza & Kudryavtseva, 1960: 258, pl. 6 (fig. 3). Collignon, 1962*a*: 95, pl. 214 (fig. 935). Dimitrova, 1967: 27, pl. 9 (fig. 3). Kotetichvili, 1970: 60, pl. 4 (fig. 3). Vašiček, 1972: 37, pl. 2 (fig. 6). Murphy, 1975: 18, pl. 2 (fig. 3).

Type

The 'holotype' is Matheron's original specimen, in the collections of the Muséum d'Histoire Naturelle de Marseille according to Murphy (1975: 18), but Matheron in fact gives three figures, and it is not clear if these represent individual specimens or composite drawings. Lectotype designation (if necessary) must await fuller redescription of the type material.

Fig. 14. *Eulytoceras phestum* (Matheron, 1878). A–C. BMNH C78698. D–E SAS L7(5). A–D, × 1; E, × 2.

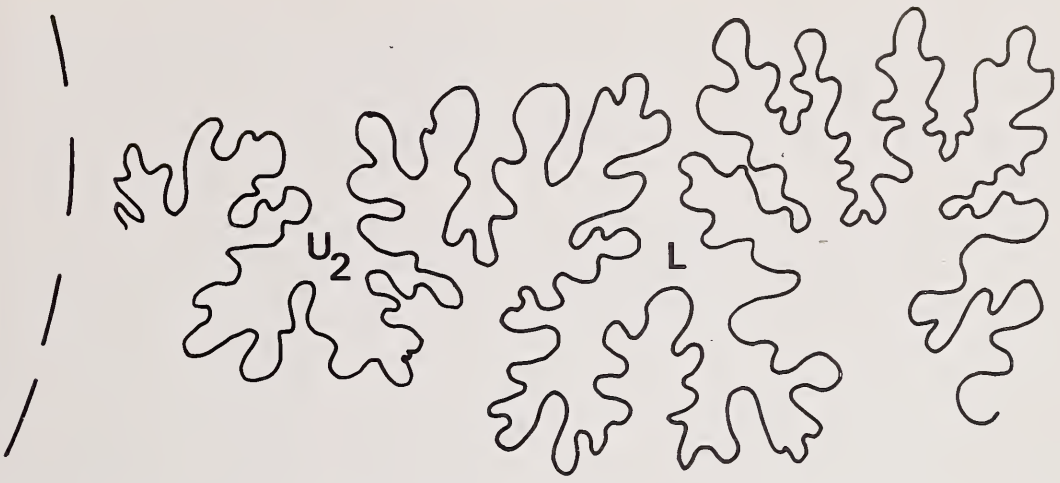

Fig. 15. Partial suture of *Eulytoceras phestum* (Matheron, 1878) based on SAS L7(5). × 8.

Material

Two specimens, SAS L7(5) and BMNH C78698, both from the Makatini Formation at locality 170, Mlambongwenya Spruit, Zululand (Barremian I).

Description

The material consists of a wholly septate juvenile 27,5 mm in diameter, and a body chamber fragment of a larger individual.

The coiling is very evolute, the whorls only just in contact, with, as a consequence, a very narrow impressed area. The coiling is evolute, the umbilicus being approximately 30 per cent of the diameter, and shallow with a rounded wall. The whorl section is as broad as high, rounded trapezoidal, with a rounded ventrolateral shoulder, convergent, somewhat flattened sides, the greatest breadth being some way beyond mid-flank, and a broadly rounded venter.

Inner whorls up to a diameter of 15 mm appear to be devoid of all ornament. Beyond this ornament consists of fine, narrow ribs separated by wide, smooth interspaces. The ribs arise at the umbilical seam, pass forwards across the umbilical wall and shoulder and are prorsiradiate and weakly flexed or convex on the flanks. Interspaces are ornamented by fine growth striae.

The external suture is partially exposed, as shown in Figure 15.

Discussion

The present specimens match closely with Matheron's original figures in terms of general ornament and proportions, his illustrations being based upon crushed specimens. *Eulytoceras phestum* is readily distinguished from *Eulytoceras inaequalicostatus* (d'Orbigny) (1840: 18, pl. 29 (figs 3–4)), for that species develops strong flares, nine per whorl in D'Orbigny's figure. *Eulytoceras raricinctum* (Uhlig) (1883: 88, pl. 5 (figs 5–7)) is a distantly ribbed form with only fifteen ribs per whorl rather than the forty to forty-two typical of *E. phestum*. *Eulytoceras rotundatum* Drushchitza (1956: 86, pl. 5 (fig. 15)) has a depressed

whorl section with fewer, more convex ribs. *Eulytoceras intemperans* (Coquand *in* Matheron) (1878, pl. c–20 (fig. 4–4c)) has only twenty-one ribs per whorl, with distinctive striae between, whilst *Eulytoceras electra* (Coquand *in* Matheron) (1878, pl. c–20 (fig 2a–2b)) has fifteen flexuous ribs per whorl, also with striae between.

The east African '*Lytoceras*' *mikadyense* (Krenkel) (1910: 223, pl. 22 (fig. 5)) is a depressed species, has periodic flares, rather irregular ribs, and prominent striae between. *Eulytoceras belchasifakaense* Collignon (1949*a*: 70, pl. 11 (fig. 2–2a), text-fig. 4), from the Hauterivian of Madagascar, has straight, quite distantly spaced ribs, rather than the slightly flexuous ornament of *E. phestum*, but may subsequently prove to be a synonym. *E.*? *komihevitraense* Collignon (1963: 15, pl. 247 (fig. 1055)), from the Middle Albian of Madagascar, is said to possess constrictions, and has dense, distinctly concave ribs with a ventral sinus. Finally, *Eulytoceras lepidum* (d'Orbigny) (1840: 149, pl. 48 (figs 3–4)) bears strong flares, and is more distantly ribbed.

Occurrence

Eulytoceras phestum is a typically Barremian species, known from southern France, the Tyrol, Czechoslovakia, Hungary, Bulgaria, the Crimea, Georgia and the Carpathians, Tunisia, Madagascar, and South Africa. Kilian & Reboul (1915: 21) also cite the species from the Lower Aptian of southern France, whilst Murphy (1975: 18) records it from the Upper Barremian of California.

Genus *Ammonoceratites* Bowdich, 1822

Subgenus *Ammonoceratites* Bowdich, 1822

Type species

Ammonoceratites lamarcki Bowdich, 1822.

Diagnosis

Large, evolute, serpenticone lytoceratids with a circular whorl section, ornamented by dense, crenulate fine ribs and growth striae, sometimes combined with faint spiral striae. Occasional broad, shallow constrictions may appear. Suture highly subdivided, with a massive cruciform septal lobe (I_s).

Discussion

A general lack of flares and associated constrictions, fine ornament and rounded whorls separates *Ammonoceratites* (*Ammonoceratites*) from *Lytoceras* Suess, 1865 *sensu stricto*, whilst lack of regular, distant flares differentiates it from *Eulytoceras* Spath, 1927, *Hemilytoceras* Spath, 1927, and *Pterolytoceras* Spath, 1927. *Ammonoceratites* (*Argonauticeras*) is readily separated by virtue of its rapidly expanding whorls and an ornament of very fine, even, generally non-crenulate ribs.

Considerable confusion surrounds the introduction of this genus, as much

as that surrounding the type species, as discussed below. Following Casey (1960: 2), *Ammonoceratites* Rafinesque, 1815, is regarded as a *nomen nudum* and *Ammonoceras* Lamarck, 1822, a *nomen dubium* (as introduced) over which *Ammonoceratites* Bowdich, 1822 (both of which have type species based on the same specimen), has priority.

The following species have been referred to the restricted subgenus:

A. (*Ammonoceratites*) *lamarcki* Bowdich (1822: 21, pl. 3 (fig. 14)).
A. (*Ammonoceratites*) *glossoidea* (Lamarck) (1822: 144 *in* Chenu 1859: 90, text-figs 391–392).
A. (*Ammonoceratites*) *mahadeva* (Stoliczka) (1865: 16, pl. 80 (fig. 1–1b)), Middle Albian of southern India.
A. (*Ammonoceratites*) *crenulatum* (Crick) (1907: 236), Upper Albian of Zululand.
A. (*Ammonoceratites*) *betiokyense* Collignon (1962*b*: 8, pl. 218 (figs 954–955)), Upper Aptian of Madagascar.
A. (*Ammonoceratites*) *crenocostatum* (Whiteaves) (1884: 45, pl. 9 (fig. 2)), Albian of British Columbia.
A. (*Ammonoceratites*) *ezoense* (Yabe) (1903: 9, pl. 1 (fig. 1), pl. 5 (fig. 1)), Upper Albian of Japan.

Occurrence

Ammonoceratites ranges from Upper Aptian to Upper Albian. There are records from British Columbia, southern France, southern India, Japan, Madagascar, and South Africa.

Ammonoceratites (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865)

Figs 16–33

? *Ammonoceratites lamarcki* Bowdich, 1822: 21, pl. 3 (fig. 14).
? *Ammonoceras glossoidea* Lamarck, 1822: 644.
? *Ammonoceratites glossoidea* Chenu, 1859: 90, text-figs 391–392.
Ammonites mahadeva Stoliczka, 1865: 165, pl. 80 (fig. 1).
Ammonites crenocostatus Whiteaves, 1876: 45, pl. 9 (fig. 2).
Lytoceras batesi Whiteaves (*non* Trask), 1884: 202, pl. 27 (fig. 1); 1900: 270.
Lytoceras mahadeva Kossmat, 1895: 17.
? *Lytoceras ezoense* Yabe, 1903: 9, pl. 1 (fig. 1), pl. 5 (fig. 1).
? *Lytoceras crenulatum* Crick, 1907: 236.
? *Lytoceras* sp. aff. *mahadeva:* Jeannet, 1908: 105–119, pls 3–6.
Lytoceras (*Ammonoceratites*) *crenulatum:* Breistroffer, 1936: 169, text-fig. 10h.
Ammonoceratites cf. *mahadeva* Collignon, 1949*b*: 45, text-fig. 6.
Ammonoceratites mahadeva: Collignon, 1963: 12, pl. 245 (fig. 1051).
Ammonoceratites crenocostatus McLearn, 1972: 22, pl. 1 (fig. 5), pl. 2 (figs 1–3).

Type

The holotype is Stoliczka's (1865, pl. 80 (fig. 1)) original specimen from the Lower Utatur Group of the environs of Moraviatoor, southern India, and presumably of Albian age. The original illustrations are reproduced here as Figures 27–28.

Material

Eight specimens: BMNH C18265, the holotype of *Lytoceras crenulatum* Crick, from the Albian of the Mzinene River area; BMNH C78890, from Bed 2 of the Mzinene Formation at locality 35 on the Mzinene River (Albian III); BMNH C78700–1, from the Mzinene Formation at locality 54 on the Mzinene River (Albian V), SAS A1195 and 2004 come from the same horizon at locality 53. SAS Z418 and Z428 in the Van Hoepen Collection are from Impala, Ndumu, Mzinene Formation (Albian II or III).

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
Holotype (after Stoliczka . . .	218,0	82,0(38)	78,0(36)	1,05	95,0(44)
A. ezoense (after Yabe)	200,0	75,0(37)	80,0(40)	0,94	70,0(35)
A. crenocostatum holotype, GSC 4987 (after McLearn) . .	44,0	14,7(33,5)	15,4(35,0)	0,95	20,7(47)
A. crenocostatum, GSC 4976 . .	—	47,0(—)	40,0(—)	1,08	— (—)
BMNH C78700 .	—	44,8(—)	41,5(—)	1,08	— (—)
	—	29,0(—)	28,0(—)	1,04	— (—)
SAS A1195, at . .	115,0	45,0(39)	44,0(38)	1,03	48,0(42)
SAS Z428, at . .	137,0	49,0(36)	48,0(36)	1,02	58,0(42)
at . .	194,0	75,0(39)	74,0(38)	1,03	83,5(43)
BMNH C78890 .	220,0	93,0(42)	88,0(40)	1,05	85,0(38)
SAS Z418 . . .	—	78,0(—)	76,0(—)	1,03	— (—)
SAS A2008 . . .	253,0	98,0(39)	96,0(38)	1,01	101,0(40)

Description

Very large (the Zululand specimens are still septate at diameters of over 300 mm), very evolute, the whorls only just in contact with a narrow, shallow dorsal impressed zone. The whorl section is almost circular, typically just slightly broader than high, the ratio varying from 1,0 to 1,05. The whorls expand quite rapidly and the umbilicus is broad, varying from 38 to 42 per cent of the diameter and increasing slightly during ontogeny, with a deeply incised umbilical seam.

Ornament changes markedly throughout growth. At the smallest diameters visible (Figs 16A, 31C) the shell surface appears virtually smooth, bearing only fine prorsiradiate growth striae, distant, minutely crenulated ribs, and occasional flares which correspond to distinct constrictions on internal moulds. Ribs, flares and striae arise at the umbilical seam, are concave on the inner part of the umbilical wall, then sweep forwards and are prorsiradiate and feebly

Fig. 16. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865). A. SAS A2004. B. BMNH C78890. × 1.

Fig. 17. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865). SAS A2004. × 0,45.

convex on inner and mid-flank (Figs 17, 20). Beyond this, the crenulated ribs become increasingly frequent, and there are sparse prominent flares and associated constrictions. In middle and later growth ribs are strong and closely spaced (Fig. 20). During these later growth stages, ribs and striae arise at the umbilical seam, sweep strongly backwards across the inner part of the umbilical wall and forwards over the umbilical shoulder. They are distinctly prorsiradiate and variably, although commonly, weakly concave across the

Fig. 18. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865). SAS A2004. × 0,45.

flanks and sweep forwards across the ventrolateral shoulder to produce a broad ventral peak of variable depth. Growth striae are scarcely visible to the naked eye, but the ribs are very distinct and strongly crenulate with a vertical apertural face and a gently inclined apical slope. On the ventral and ventrolateral region of some of the Zululand specimens there are distinct, curved longitudinal striae between and connecting the crinkled ribs, arising from individual crinkles (Fig. 20).

Partially exfoliated shells show low, broad, irregular, fold-like constricted

Fig. 19. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865). SAS 2418. × 1.

Fig. 20. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865). BMNH C78890. × 0,6.

areas during middle and later growth (Figs 22–23), and in some places, transverse rows of large pits corresponding to the site of crinkled ribs. Weathered shell surfaces are also covered in minute pits. Internal moulds are essentially smooth, save for broad, shallow, fold-like constrictions (Fig. 19).

One specimen shows a dorsal callus, through which traces of the underlying ventral ornament are still visible.

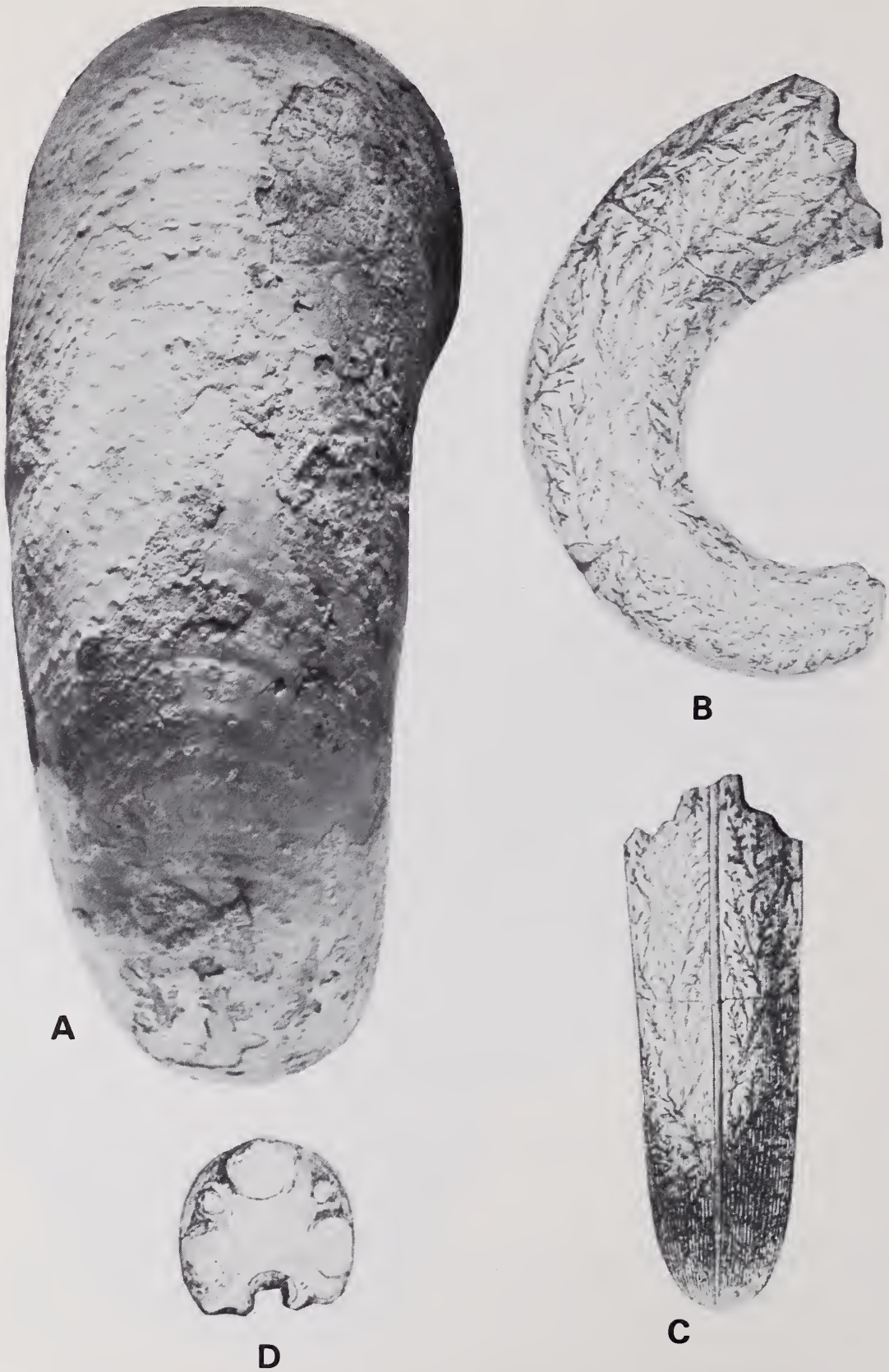

Fig. 21. A. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865). BMNH C78890. × 0,6. B–D. *Ammonoceratites lamarcki* Bowdich. Copy of Chenu 1859, text-fig. 391.

Fig. 22. The holotype of *Ammonoceratites* (*Ammonoceratites*) *crenulatum* (Crick, 1907). BMNH C18265. Slightly reduced.

The suture line is highly subdivided with a long spatulate ventral saddle, a large bifid asymmetric E/L saddle and a smaller also asymmetrically bifid L/U_2 saddle, separated by a very large lateral lobe (L), deeper than the external lobe (E) and bifid, with a large subdivided median element. U_1 is highly subdivided, dorsal internal lobe (I) cruciform, septal lobe large (Fig. 18).

Discussion

The Zululand specimens show some variation in strength and direction of ornament and relative proportions when compared with Stoliczka's magnificent

Fig. 23. The holotype of *Ammonoceratites* (*Ammonoceratites*) *crenulatum* (Crick, 1907). BMNH C18265. Slightly reduced.

specimen. In particular, the ventral peak is more prominent than shown in his figure and the ribs are prorsiradiate rather than radial. The material varies in these respects, and rather than trying to separate it into *Ammonoceratites mahadeva* with straight ribs and a shallow ventral peak and *Ammonoceratites crenulatum*, with prorsiradiate ribs and a deeper peak, the authors regard their material as one variable species. It is, however, far from clear whether *Ammonoceratites mahadeva* is the earliest name used for this species.

Lamarck (1822, vol. 7: 644) introduced the name *Ammonoceras glossoidea*,

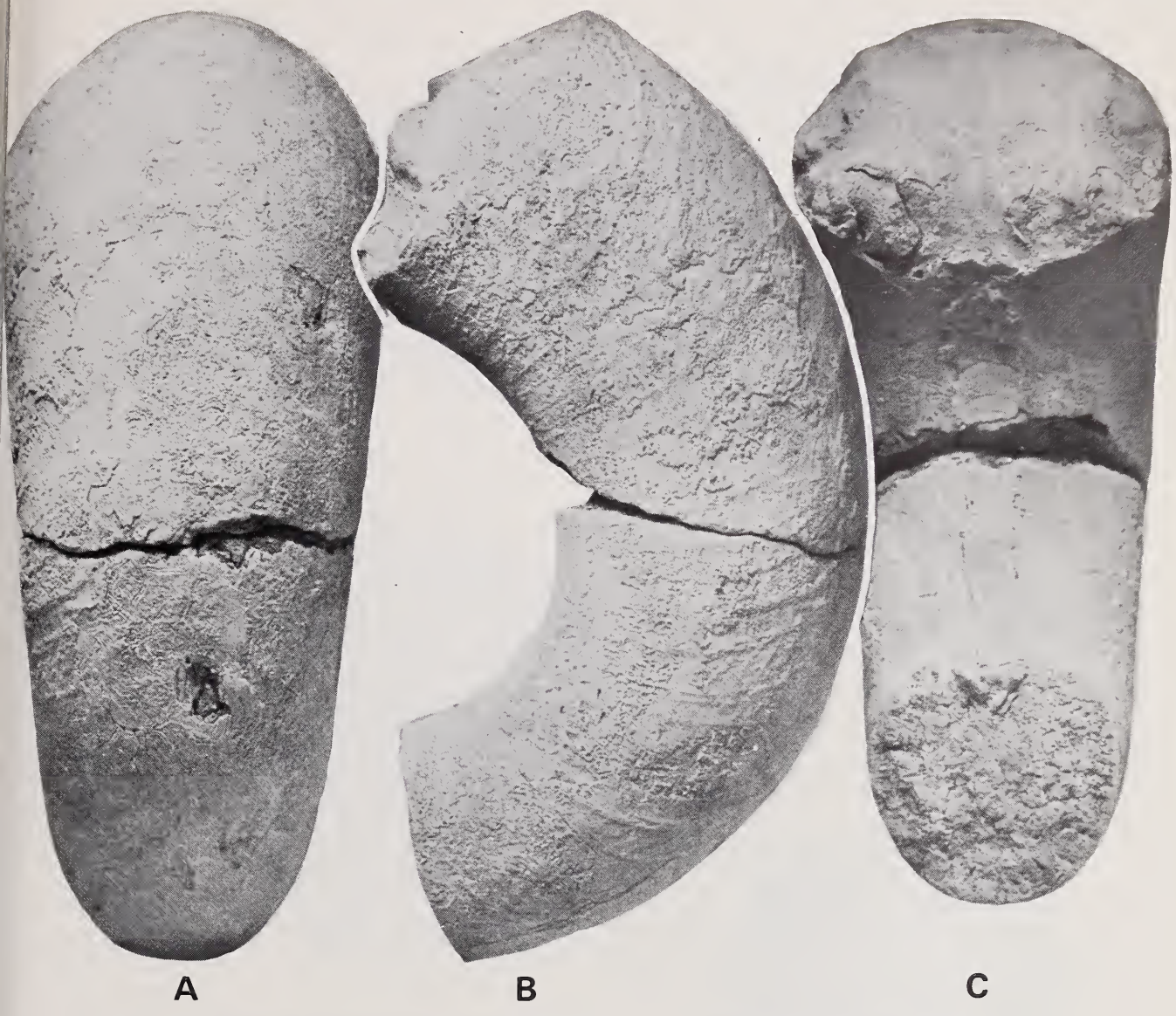

Fig. 24. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865). BMNH C78700. × 1.

without figuring the material. His description is brief: 'Cette coquille rompue en trois morceaux, qui s'appartiennent successivement, et dont l'un offre l'extrémité supérieure de cette mème coquille, est d'une assez grande taille, fort épaisse en sa partie inférieure, arcuée presque en demi-cercle, et se termine supérieurement en forme de langue. Ses loges sont remplies de matière pierreuse, et leurs cloisons ne se distinguent que dans les parois où leurs concours forment des sutures lobées, laciniées, rameuses, tout à fait analogues à celles des ammonites. Mais la coquille dont il s'agit en est très-distincte par sa forme générale; car malgré son arcuation, elle n'eût point forme de tours contigus, si la nature l'eût agrandie davantage. Sa longueur est de cinquante centimètres.'

In the same year, Bowdich (1822: 21, pl. 3 (fig. 14)) introduced the name *Ammonoceratites lamarcki*, based upon the same fragments. His description is

Fig. 25. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865). BMNH C78700. × 1.

Fig. 26. External suture of *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865). BMNH C78890. × 1,6.

also brief: 'Septa numerous, undulated at the margins, pl. 3, fig. 14. Siphon marginal, interior. Rolled on itself in the same plane? The locality is unknown, M. Lamarck purchased it by accident: he kindly allowed me to take it home in order that the figure, the first that has been made, might be as accurate as possible.'

Subsequent authors have varied in their views of the nature of *Ammonoceras glossoidea*—*Ammonoceratites lamarcki* (the latter has priority; *fide* Casey 1960), regarding it as of both Jurassic and Cretaceous age and as a species of *Hamites*, *Toxoceras*, and *Pictetia*. The age is, however, in all probability Cretaceous, for as Chenu (1859: 90) notes, the specimen was not purchased by Lamarck, for he (Chenu) quotes Valenciennes as telling him that 'Lamarck lui a souvent répété que ce fossile, dont il faisait grand cas, avait été rapporté par le secrétaire de la colonie de Pondichéry, et donné au fils de Buffon, qui lui en avait luimême fait cadeau. M. Valenciennes ajoute que parmi les ammonites rapportées de l'Inde par Jacquemont, il se trouve aussi un fragment de l'A. fimbriatus.'

Chenu's figure is much better than that of Bowdich, and is reproduced here as Figure 21B–D. The specimen was said to be 500 mm in diameter, and corresponds to the generally accepted interpretation of *Ammonoceratites*; its occurrence in southern India indicates that it may well be a specimen of what has subsequently been termed *Ammonoceratites mahadeva*. The figures are,

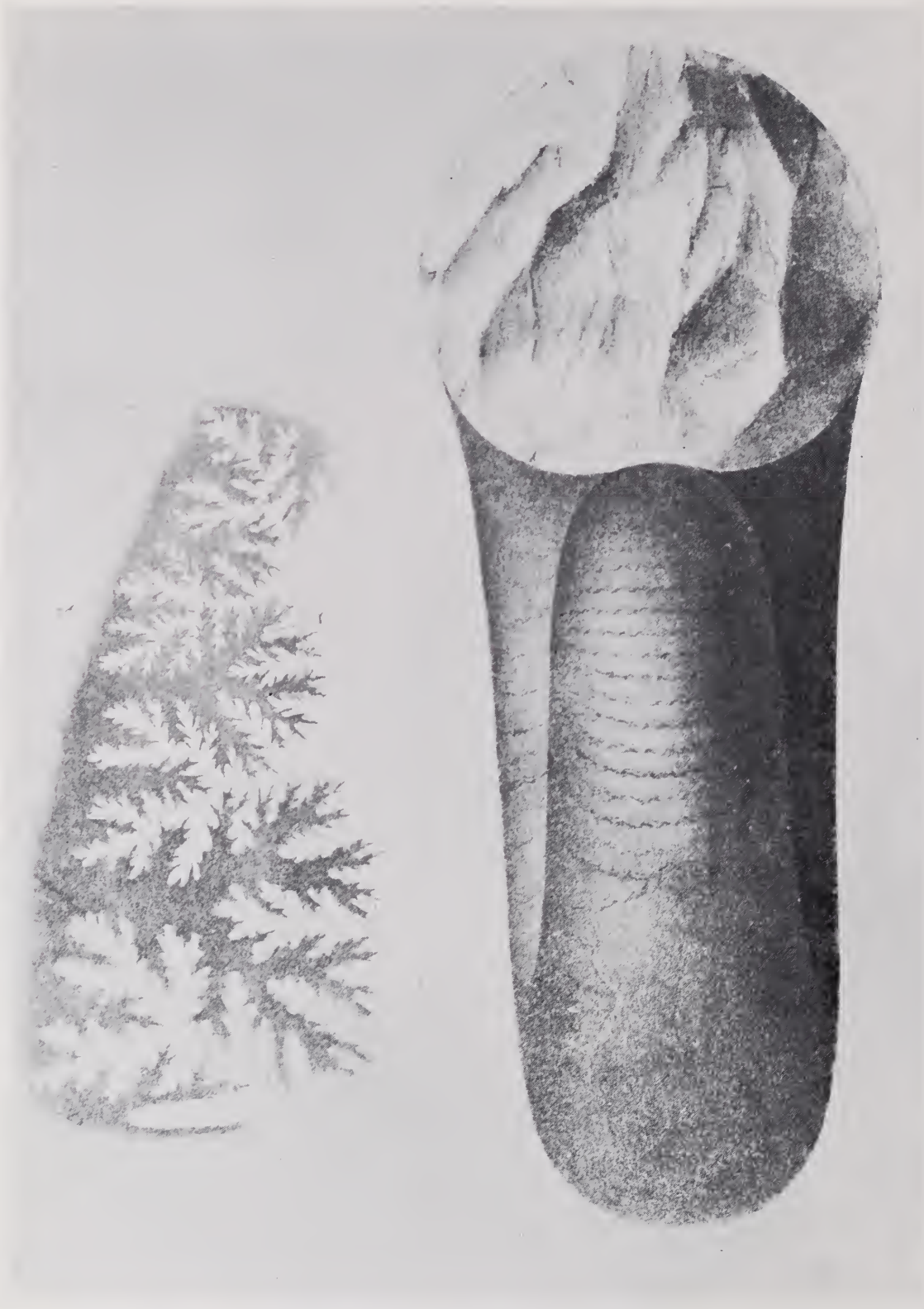

Fig. 27. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1861). Copy of Stoliczka's figures of the holotype, reduced here by approximately 0,75.

Fig. 28. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1861). Copy of Stoliczka's figure of the holotype, reduced here by approximately 0,75.

however, so poor that, until the specimen is redescribed and refigured, the authors would prefer to use Stoliczka's name, having sought without success for the Lamarck/Bowdich type in the Paris museums.

Of other species, *Ammonoceratites* (*Am.*) *betiokyense*, from the Aptian of Madagascar, is based on two small fragments only, but appears to have distinctly flattened sides and a markedly asymmetric or even subtrifid U_2 lobe

Fig. 29. *Ammonoceratites* (*Ammonoceratites*) *ezoense* (Yabe, 1903). Lectotype. × 0,75.

according to Collignon (1962*b*: 8).

Ammonoceratites (*Am.*) *ezoense* (Yabe), lectotype, herein designated, Yabe's (1903: 9, pl. 1 (fig. 1), pl. 5 (fig. 1)) original specimen is also an Albian species (see range charts in Matsumoto 1954), the original material being preserved in the collections of the Geology Department of Tokyo University, and refigured here as Figures 29–30, 31A–B. Yabe separated it from *Ammo-*

Fig. 30. *Ammonoceratites* (*Ammonoceratites*) *ezoense* (Yabe, 1903). Lectotype. × 0,75.

noceratites (*Am.*) *mahadeva* on the basis of more rapidly expanding whorls and a smaller umbilicus (Yabe's measurements are reproduced above), but as can be seen from the present photographs, the preservation is poor and the specimen probably within an acceptable range of variation for *A.* (*Am.*) *mahadeva* as shown by the Zululand specimens (e.g. compare Figs 29–30, 31A–B with Figs 17–19); the authors therefore place it as a questionable synonym.

Fig. 31 A–B. *Ammonoceratites* (*Ammonoceratites*) *ezoense* (Yabe, 1903). Part of lectotype, showing suture. C. *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1861); inner whorls of SAS A2004. × 1,5.

Ammonoceratites (*Am.*) *crenocostatus* (Whiteaves) is a further Middle? to Upper Albian species known only from the Queen Charlotte Islands off the coast of British Columbia. The authors have been able to examine casts of the holotype and other specimens from the area, illustrated here as Figures 32–33.

The holotype is only 43 mm in diameter, and it retains only part of the shell. The inner whorls are strongly constricted on the mould up to a diameter of 20 mm, with traces of delicate striae where shell is preserved; from 20 to 40 mm there are distant fine ribs with delicate growth striae between, both ribs and striae being prorsiradiate and feebly convex on the venter. Over the last preserved part of the specimen the ribs crowd markedly. GSC 4976 is a larger specimen, with an original diameter of approximately 120–130 mm. The outer whorl shows distinctly concave prorsiradiate flank ribs, with a marked convex ventral peak, rib density, form and strength matching closely to the similarly sized Zululand specimen BMNH C78700 (Figs 24–25). So far as can be judged there are no criteria that can be used to separate *A.* (*Am.*) *crenocostatum* from the Zululand material, and it is therefore suggested that it is a further synonym of *Ammonoceratites* (*Am.*) *mahadeva*.

Occurrence

As defined above, *Ammonoceratites* (*Am.*) *mahadeva* ranges from Middle to Upper Albian, and is known from southern India, the Queen Charlotte Islands, Madagascar, Japan, Zululand, and perhaps the Jura (Jeannet 1908: 105–119, pls 3–6).

Subgenus *Argonauticeras* Anderson, 1938

Type species

Lytoceras argonautarum Anderson, 1902.

Diagnosis

A subgenus of *Ammonoceratites* with a high expansion rate, subrectangular to trapezoidal whorl section, fine, equal, dense, straight to gently flexed ribs or striae without obvious crinkles. Weak, broad constrictions may be present on early whorls.

Discussion

Argonauticeras can be separated from other Cretaceous lytoceratid genera by its fine, even, typically non-crenulate ornament and high expansion rate. The trapezoidal whorl section, emphasized by Wright (in Arkell & Wright 1957), is a less distinctive feature, as discussed below. Differences from *Ammonoceratites* (*Ammonoceratites*) are outlined above.

Four species have been referred to the subgenus:

Argonauticeras argonautarum (Anderson) (1902: 85, pl. 7 (figs 154–155); 1938: 149, pl. 17 (fig. 3), pl. 19 (figs 1–2)). Upper Aptian of California.

Fig. 32. *Ammonoceratites* (*Ammonoceratites*) *crenocostatus* (Whiteaves, 1876). Holotype, GSC 4987. × 2.

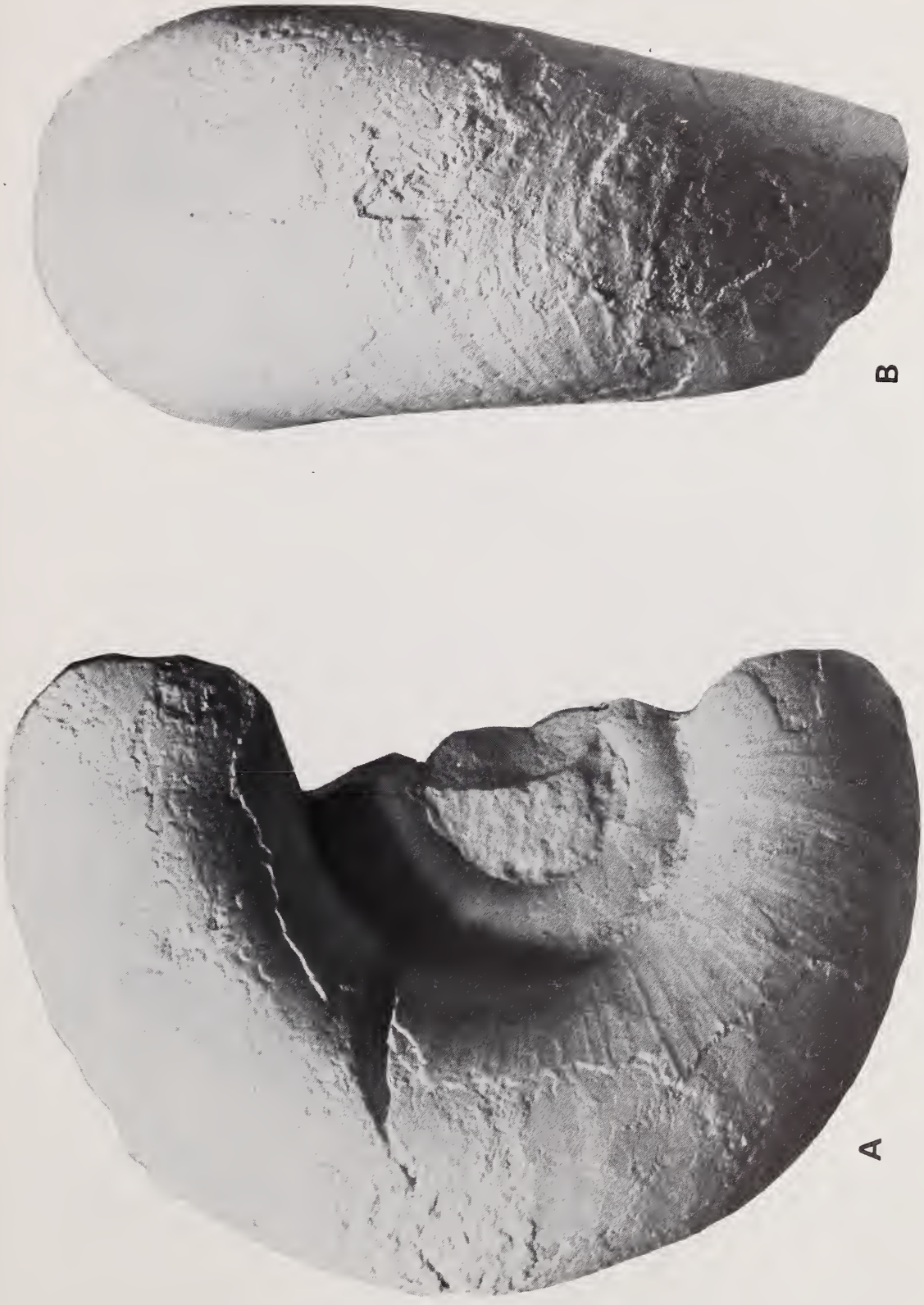

Fig. 33. *Ammonoceratites* (*Ammonoceratites*) *crenocostatus* (Whiteaves, 1876). Hypotype, GSC 4976. × 1.

Argonauticeras depereti (Kilian) (1892: 8, pl. 1 (fig. 2). Thomel, 1968: 684–687, pl. 35 (figs 1–4)). Upper Aptian of southern France.

Argonauticeras besairiei Collignon (1949*b*: 46, pl. 8 (fig. 1)). Upper Aptian to Middle Albian of Madagascar.

Argonauticeras belliseptatum (Anthula) (1899: 97, pl. 6 (fig. 1), pl. 7 (fig. 1)). Aptian of the Caucasus and Madagascar.

Of these species, Dimitrova (1967: 28, pl. 10 (fig. 6)) figured a fragment referred to as *Pictetia belliseptata* (Anthula) which appears actually to uncoil. The authors therefore take the opportunity to figure photographically the holotype of *A.* (*Ar.*) *belliseptatum* (Figs 40–43) which shows it to be an *Argonauticeras*.

Pseudotetragonites Drushchitza, 1956 (type species *P. kudrjavzevi* Drushchitza), is a subjective synonym of *Argonauticeras*, based on juveniles.

Occurrence

Argonauticeras is known from the Upper Aptian of southern France, the Caucasus, California, the Lower and Middle Albian of Madagascar, and the Middle Albian of Zululand.

Ammonoceratites (*Argonauticeras*) *depereti* (Kilian, 1892)

Figs 34–37, 38B, 39–43

Lytoceras depereti Kilian, 1892: 8, pl. 1 (fig. 2a–b). Simionescu, 1900: 656.
Lytoceras belliseptatum Anthula, 1899: 97, pl. 6 (fig. 1), pl. 7 (fig. 1). Collignon, 1963: 12, pl. 245 (fig. 1052).
Lytoceras argonautarum Anderson, 1902: 85, pl. 7 (figs 154–155).
Tetragonites depereti Jacob, 1907: 12. *Non* Fallot, 1920: 243, pl. 2 (fig. 5), text-fig. 13.
Lytoceras (*Argonauticeras*) *argonautarum*: Anderson, 1938: 140, pl. 17 (fig. 3), pl. 19 (figs 1–2).
Pseudotetragonites kudrjavzevi Drushchitza, 1956: 80, pl. 7 (fig. 25), text-fig. 35. Orlov, 1958: 58, pl. 20 (fig. 4), Drushchitza & Kudryavtseva, 1960: 257, pl. 5 (fig. 2a–b), text-fig. 64.
Ammonoceratites (*Argonauticeras*) *depereti* Collignon, 1956: 100. Thomel, 1968: 684, pl. 35 (figs 1–4), text-figs.
? *Pictetia belliseptata* Dimitrova, 1967: 28, pl. 10 (fig. 6).
Argonauticeras belliseptatum Förster, 1975: 144, pl. 1 (fig. 6).

Type

The lectotype, herein designated, is Kilian's original specimen from the Upper Aptian of the environs of Barrême (Basses Alpes), south-eastern France, in the collections of Muséum d'Histoire Naturelle, Lyon.

Material

Two specimens, UPG B4 and UPG B5 from the Makatini Formation, Upper Aptian, Manyola Drift on the Usutu River, at 26°49′15″ S 30°13′30″ E.

Fig. 34. *Ammonoceratites* (*Argonauticeras*) *depereti* (Kilian, 1892). UPG B4. × 0,78.

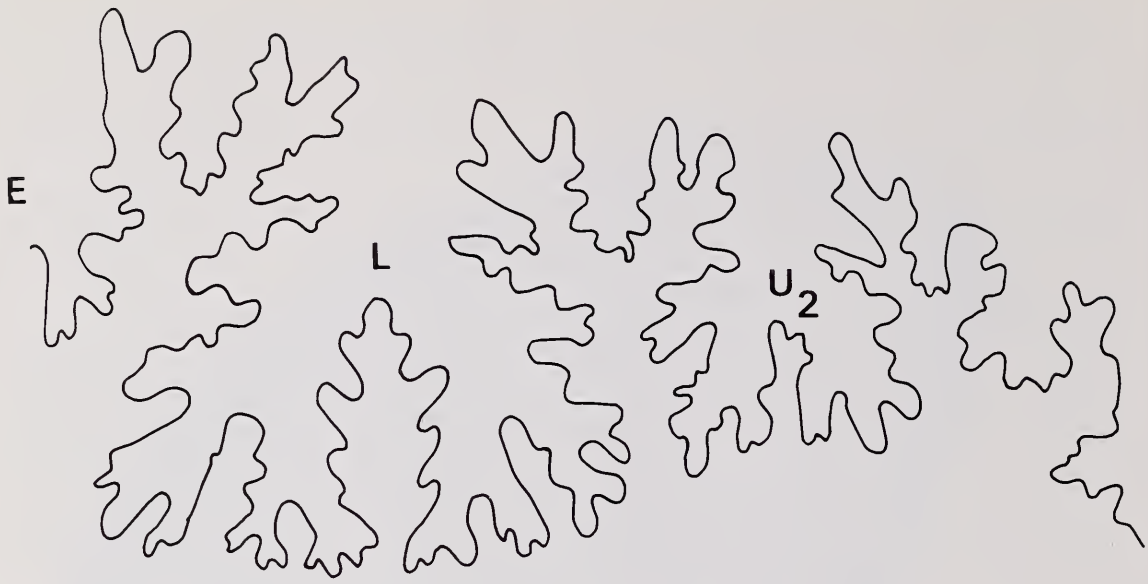

Fig. 35. External suture of *Ammonoceratites* (*Argonauticeras*) *depereti* (Kilian, 1892). × 0,8.

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
Californian specimen (after Anderson, 1938)	250,0	125,0(50)	113,0(45)	1,11	87,0(35)
Holotype of *A.* (*Ar.*) *belliseptatum* (after Anthula, 1899) .	325,0	153,0(47)	130,0(40)	1,17	123,0(38)
Lectotype of *A.* (*Ar.*) *depereti* (after Kilian, 1892) . .	53,0	25,0(47)	27,0(39)	1,19	21,0(39)
French specimens (after Thomel, 1968)					
151	38,3	19,3(50)	16,0(41)	1,20	14,4(37)
152	55,0	27,0(49)	23,0(41)	1,17	19,2(34)
153	102,0	43,0(42)	44,5(43)	0,96	38,0(36)
UPG B4	179,0	70,0(39)	67,0(27)	1,04	73,0(40)
UPG B5	—	40,0(—)	37,0(—)	1,08	— (—)

Description

The largest specimen in the collection consists of one and a half whorls, parts of which are damaged. Coiling is very evolute, and whorls increase rapidly in height and width. The whorl section is slightly wider than high with rounded umbilical and ventrolateral edges; the dorsal impressed zone is small.

Ornament consists of narrow, dense unbranched ribs which pass forwards over the flanks with a slight curvature and straight across the venter. Broad,

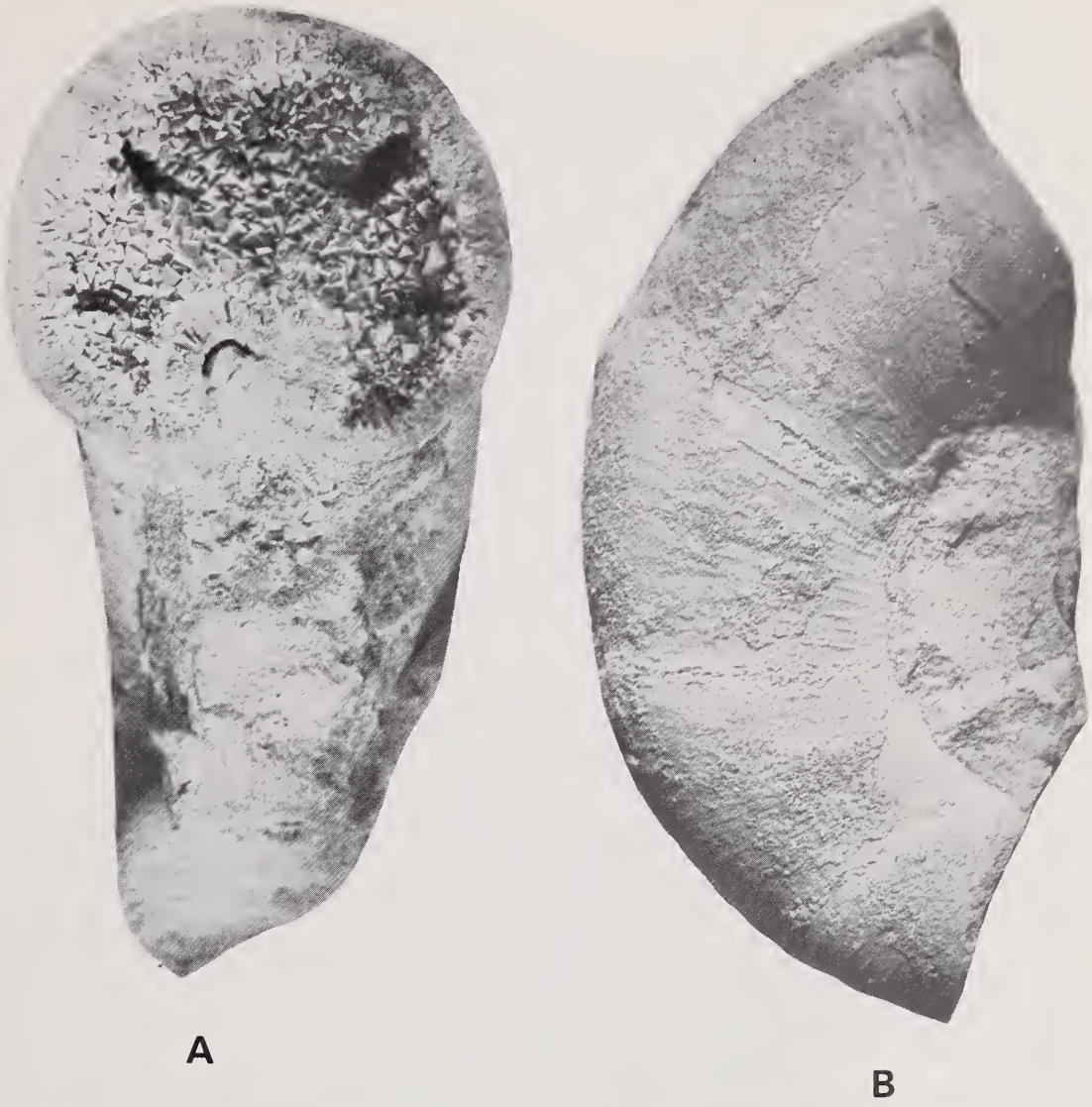

Fig. 36. *Ammonoceratites* (*Argonauticeras*) *depereti* (Kilian, 1892). UPG B5. × 1.

low constrictions are also present, paralleling striae; the number of constrictions per whorl cannot be determined, but on the smaller specimen, UPG B5, there are four equidistant constrictions in one-third of a whorl. The suture is only partially exposed; E is narrow and bifid, L is very wide and deeper than both E and U_2. The saddles E/L and I/U_2 are bifid and have slender stems.

Discussion

Thomel recently (1968) reviewed this species and pointed to the changes in whorl section, relative dimensions and density of ornamentation during ontogeny. The Zululand specimens fall within the range of relative proportions given by Thomel (1968: 685) and are virtually identical to the figured specimens as far as the whorl section, fine ornamentation and constrictions are concerned. The largest known French specimen of *A.* (*Ar.*) *depereti* is only 102 mm in

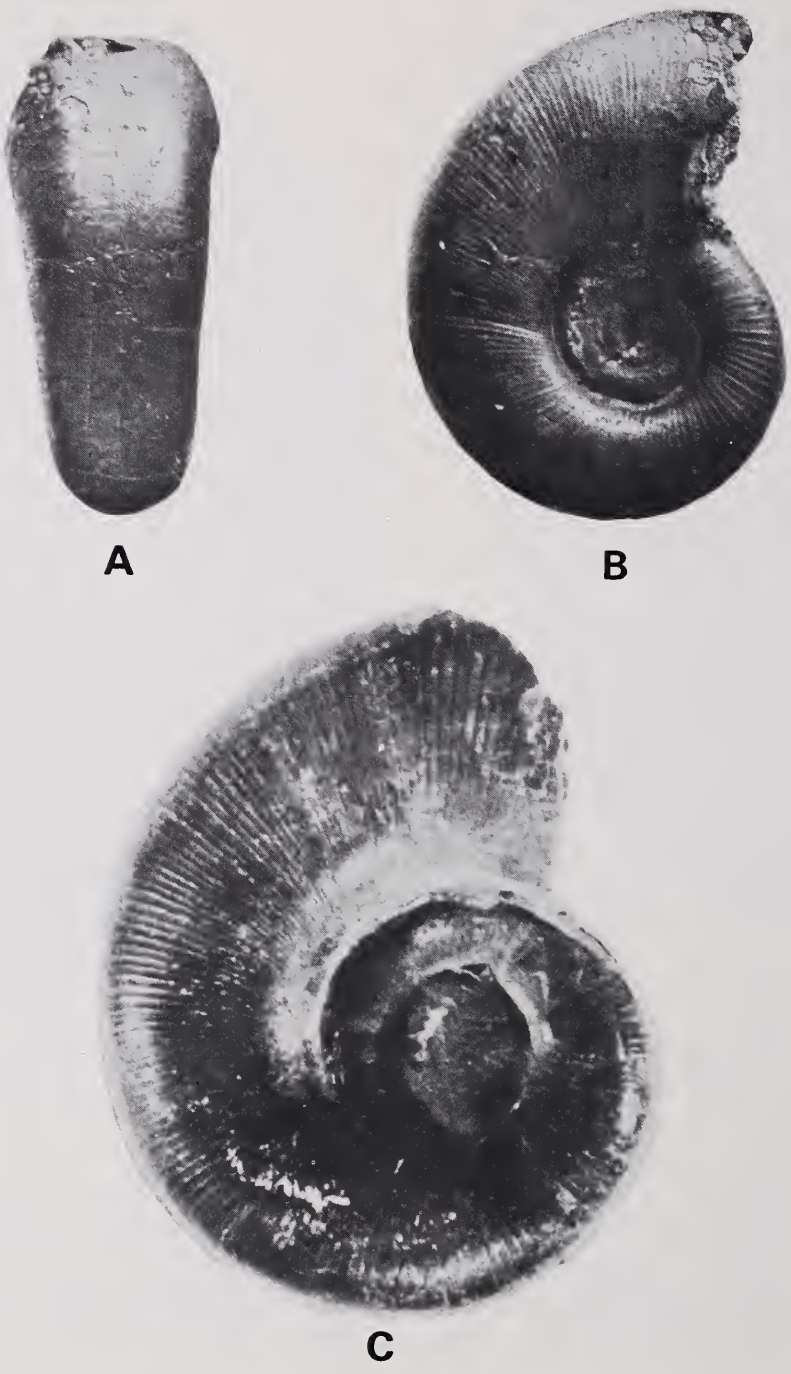

Fig. 37. *Ammonoceratites* (*Ammonoceratites*) *depereti* (Kilian, 1892). A–B. Copies of Kilian's figures of the holotype. C. Copy of Anderson's (1938: pl. 17 (fig. 3)) figure of a juvenile *Lytoceras* (*Argonauticeras*) *argonautarum* (Anderson, 1902). All figures × 1.

Fig. 38. A. *Ammonoceratites* (*Argonauticeras*) aff. *depereti* (Kilian, 1892). UPG B465. × 1. *B. Ammonoceratites* (*Argonauticeras*) *depereti* (Kilian, 1892). UPG B4. × 1.

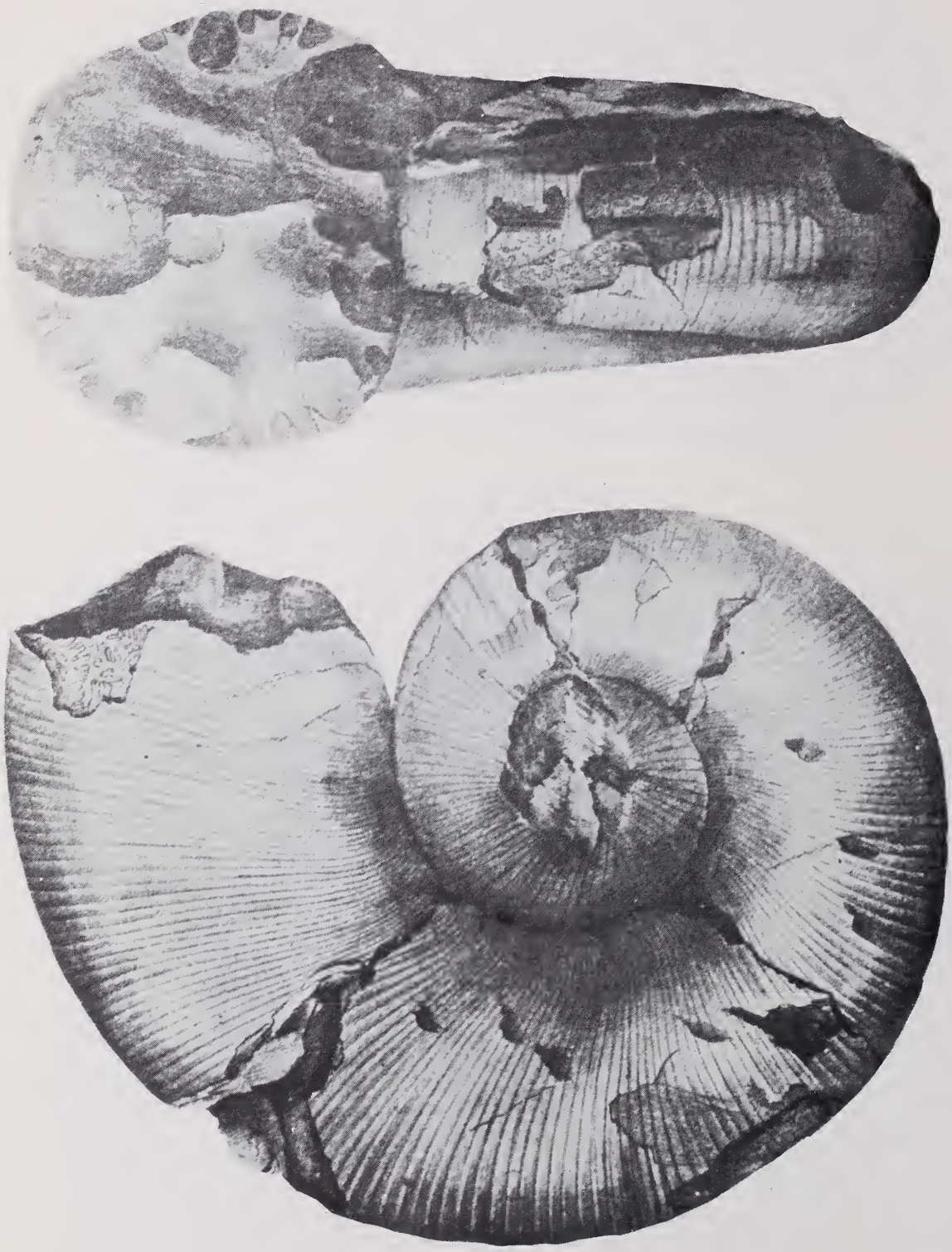

Fig. 39. *Ammonoceratites* (*Argonauticeras*) *argonautarum* (Anderson, 1902). Copies of Anderson's original figures of the species. × 0,75.

Fig. 40. *Ammonoceratites* (*Argonauticeras*) *belliseptatum* (Anthula, 1899). Holotype. × 0,45. (Photograph supplied by R. A. Reyment.)

Fig. 41. *Ammonoceratites* (*Argonauticeras*) *belliseptatum* (Anthula, 1899). Holotype. × 0,45. (Photograph supplied by R. A. Reyment.)

Fig. 42. *Ammonoceratites* (*Argonauticeras*) *belliseptatum* (Anthula, 1899). Holotype. × 0,45. (Photograph supplied by R. A. Reyment.)

Fig. 43. *Ammonoceratites* (*Argonauticeras*) *belliseptatum* (Anthula, 1899). Holotype. × 0,45. (Photograph supplied by R. A. Reyment.)

diameter, and thus difficult to compare with the holotype of *Argonauticeras argonautarum* (Anderson), the original figures of which are reproduced here as Figure 39. A smaller specimen figured subsequently by Anderson (1938: pl. 17 (fig. 3)) is reproduced here as Figure 37C; it appears identical to Kilian's lectotype (reproduced here as Fig. 37A–B), and in consequence the authors regard *A.* (*Ar.*) *argonautarum* as a junior subjective synonym of *A.* (*Ar.*) *depereti*. *A.* (*Ar.*) *belliseptatum* Anthula is based on a giant disc 325 mm in diameter. When compared with the present material, the overall proportions, expansion rate, style and direction of ornament are so similar that the authors believe this to be a synonym of *A.* (*Ar.*) *depereti*. The remaining species referred to the subgenus, *A.* (*Ar.*) *besairiei* Collignon (1949*b*: 46, pl. 8 (fig. 1)), is also very similar, and, indeed, Förster (1975: 144) regarded it as a synonym of *A.* (*Ar.*) *belliseptatum*. The juvenile holotype has, however, a distinctly trapezoidal whorl section with a broad, flattened venter, flattened flanks and, according to Collignon, has straight and rather coarse ribs for the genus. A larger Madagascan specimen figured subsequently (Collignon 1962*b*: 10, pls 219–220 (fig. 956)) has a very high expansion rate, the proportions (after Collignon) being:

D	*Wb*	*Wh*	*Wb:Wh*	*U*
270,0	160,0(58)	136,0(48)	1,18	82,0(30)

Given a larger sample it might prove possible to demonstrate that *A.* (*Ar.*) *besairiei* is also within the range of variation of *A.* (*Ar.*) *depereti*, but the authors maintain the species separate at this time whilst acknowledging the fine division between them.

Occurrence

As defined above, *Ammonoceratites* (*Argonauticeras*) *depereti* is known from the Upper Aptian of the Caucasus, Bulgaria, southern France, California, Mozambique and Zululand, and the Albian of Madagascar.

Ammonoceratites (*Argonauticeras*) aff. *depereti* (Kilian, 1892)

Figs 38A, 44–46

Material

One specimen only, UPG B465, from the Mzinene Formation, Albian III–IV, Mlambongwenya Spruit, northern Zululand.

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
UPG B465 . . .	47,5	23,5(49)	21,0(44)	1,12	— (—)
	84,0	40,0(48)	38,5(46)	1,04	— (—)
	149,0	68,5(46)	67,5(45)	1,02	— (—)
	248,0	99,5(40)	98,5(40)	1,01	— (—)
	352,0	127,5(36)	134,0(38)	0,97	135,0(38)

Fig. 44. *Ammonoceratites* (*Argonauticeras*) aff. *depereti* (Kilian, 1892). UPG B465. × 0,5.

Fig. 45. *Ammonoceratites* (*Argonauticeras*) aff. *depereti* (Kilian, 1892). UPG B465. × 0,5.

Description

The specimen is beautifully preserved, retaining part of the original shell. All but the last quarter whorl are septate.

Coiling is very evolute with the whorls increasing gradually in height and width. The dorsal area of impression is very shallow. The whorl section varies with increasing diameter as shown in the table of dimensions. It is initially rectangular, but with increasing diameter the venter becomes narrower and the whorl height becomes greater than the whorl breadth. Maximum whorl breadth is at the dorsal third of the flanks. The surface is ornamented by numerous thin,

Fig. 46. Suture of *Ammonoceratites* (*Argonauticeras*) aff. *depereti* (Kilian, 1892). UPG B465. × 3,6.

fine ribs. The ribs pass radially over the umbilical wall and then forwards across the flanks with a slight curvature, and straight over the venter. On the venter of one of the inner whorls, where the specimen had been broken, the ribs are minutely crinkled and are connected longitudinally by faint striae. At a whorl height of 63 mm there are 45 ribs in a distance equal to the whorl height; at 85 mm the figure is 42. On the inner whorls the flanks bear low folds, so that the ribs appear to bunch. On the outer whorls this effect is less noticeable, but two wide and shallow, barely noticeable constrictions occur. The external suture (Fig. 46) is highly divided with narrow-stemmed saddles. The lobes are asymmetrically bifid.

Discussion

As can be seen from the dimensions, the ratio of Wb/Wh decreases with increase in diameter, a situation somewhat comparable to that encountered in *A.* (*Ar.*) *depereti*, from which it differs in the lack of constrictions on inner whorls (Fig. 38A), as a consequence of which the authors refer to it as *A.* (*Ar.*) aff. *depereti*. It is readily separated from *A.* (*Ar.*) *besairiei* which is markedly depressed at large diameters.

Occurrence

Middle Albian of northern Zululand.

Ammonoceratites (*Argonauticeras*) *besairiei* Collignon, 1949

Figs 47–48A

Argonauticeras besairiei Collignon, 1949*a*: 46, pl. 8 (fig. 1); 1950: 36, pl. 5 (fig. 6); 1962*b*: 10, pl. 219–220 (fig. 956).

Holotype

The original of Collignon (1949*a*: pl. 8 (fig. 1)), a juvenile specimen from the Lower/Middle Albian transition beds of Ambarimaninga, Madagascar.

Material

A single fragment, BMNH C78697, from the Mzinene Formation, Albian III, of locality 171, Mlambongwenya Spruit, northern Zululand.

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
Holotype (after Collignon, 1949*a*)	43,0	21,0(49)	18,0(42)	1,17	16,0(37)
Specimen 1 of Collignon, 1950 .	70,0	35,0(50)	33,0(47)	1,06	26,0(35)
Specimen 2 of Collignon, 1950 .	130,0	51,0(50)	48,0(47)	1,06	28,0(27)
Original of Collignon, 1962*b*: pls 219–220 (fig. 956)	200,0	106,0(53)	94,0(47)	1,13	63,0(32)
BMNH C78697 .	—	121,0(—)	107,0(—)	1,13	— (—)

Description

The specimen is a wholly septate fragment of a large, massive ammonite whose original diameter must have been well over 200 mm. The coiling is very evolute, with a narrow, shallow impressed area. The umbilicus is of moderate size, and deep. The whorls expand rapidly and are depressed, rounded-trapezoidal, the greatest breadth being well below mid-flank. The umbilical wall is high, rounded, merging with broadly rounded umbilical shoulders and lower flanks. The upper flanks are flattened and converge to a broadly rounded venter.

Ornament consists of fine, non-crenulate, narrow, flattened ribs separated by wider interspaces. These arise at the umbilical seam, sweep abruptly back across the lower part of the umbilical wall and curve forwards over the shoulder to pass across the flanks in a rectiradiate or slightly prorsiradiate direction, with a faint convexity. They pass straight across the venter.

The external suture is not visible, but the fractured sections indicate the presence of large L and U_2 lobes, together with a large septal lobe. The dorsum shows the impression of the venter of the penultimate whorl, which was distinctly flattened.

Discussion

At the diameter represented by the Zululand specimen, the trapezoidal whorl section of *Argonauticeras* is lost, but when compared with the series of specimens of *A.* (*Argonauticeras*) *besairiei* figured by Collignon (1949*a*–1962*b*), the present specimen is clearly an adult of that species.

Occurrence

Upper Aptian to Middle Albian of Madagascar, Middle Albian of Zululand.

Fig. 47. *Ammonoceratites* (*Argonauticeras*) *besairiei* Collignon, 1949. BMNH C78697. × 0,7.

Genus *Protetragonites* Hyatt, 1900

Type species

Ammonites quadrisulcatus d'Orbigny, 1841.

Diagnosis

Very evolute lytoceratids with circular to oval whorl sections, sparse to frequent radial or curved constrictions and a shell ornamented by growth striae only.

Discussion

Repeated attempts have been made to justify a separation of a family Protetragonitidae Spath, 1927, from the Lytoceratidae. This has been based on the tendency for species to develop one or more auxiliary elements in the suture line. Schindewolf (1960: 681) and Wiedmann (1962: 17) have both demonstrated that *Protetragonites* follow the same sutural development as the Lytoceratidae, and are derived from *Lytoceras sensu stricto*. The authors further follow Schindewolf and Wiedmann in regarding *Hemitetragonites* Spath, 1927, and *Leptotetragonites* Spath, 1927, as subjective synonyms.

Occurrence

Protetragonites is a typically Mesogean genus, known chiefly from the Mediterranean region, but also known from central Europe (Austria), the Crimea, Caucasus, north Africa, Madagascar, and now Zululand. Its stratigraphic range is from Tithonian to Upper Albian.

Protetragonites aeolus aeolus (d'Orbigny, 1850)

Fig. 48B–F

Ammonites aeolus d'Orbigny, 1850: 125.
Lytoceras (*Gaudryceras*) *aeolus* Jacob, 1908: 14 (pars), pl. 1 (fig. 17), *non* pl. 1 (figs 14–16).
Gaudryceras aeolus: Fallot, 1920: 12. Collignon, 1949*b*: 50.
Hemitetragonites aeolus Breistroffer, 1936: 175. Breistroffer & Villoutreys, 1953: 71 (pars).
Protetragonites aeolus aeolus Wiedmann, 1962: 24, pl. 10 (fig. 3), text-fig. 6.
Protetragonites aeolus: Wiedmann & Dieni, 1968: 31.

Type

The lectotype, designated by Wiedmann (1962: 25), is MNHP 5770 in the D'Orbigny Collection, Muséum d'Histoire Naturelle, Paris, and is from the Middle? Albian of Escragnolles, Var, France.

Material

Two specimens, SAS PJR/1–2, from the Mzinene Formation, Albian V, at locality 65 along the Munywana Creek, east of Hluhluwe, Zululand, are definitely referred to the subspecies, whilst a third specimen, BMNH C78699, from the same horizon at locality 56 on the Mzinene River, may also belong here.

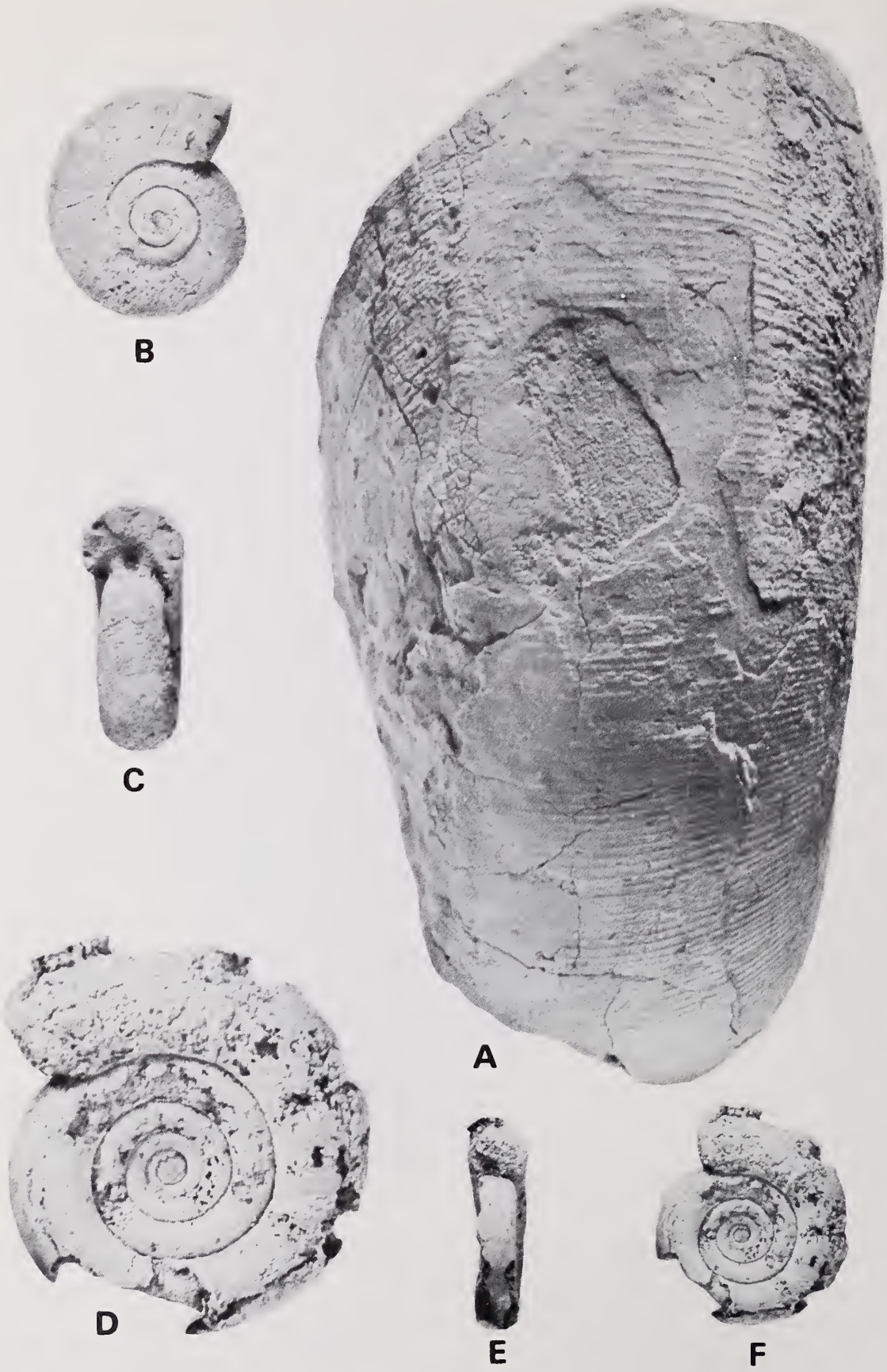

Fig. 48. A. *Ammonoceratites* (*Argonauticeras*) *besairiei* Collignon, 1949. BMNH C78697. × 0,7. B–F. *Protetragonites aeolus aeolus* (d'Orbigny). B–C. PJR/1. D–F. BMNH C78699. B–C, × 1; D, × 2; E–F, × 1.

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
Lectotype, MNHP 5770	31,0	12,5(40)	10,5(34)	1,19	14,5(47)
PJR/1	30,7	12,5(41)	8,7(28)	1,43	14,3(47)
BMNH C78699 (approximate)	30,1	— (—)	9,3(31)	—	15,0(50)

Description

The coiling is very evolute, serpenticone, with a very wide umbilicus (47–50% of diameter). The whorl section is depressed, reniform, with a gently rounded venter and swollen flanks (the greatest breadth is below mid-flank). The dorsal impressed zone is narrow and shallow.

All specimens are corroded and no external shell surface survives except in a few areas which retain a suggestion of growth striae. There are four straight, prorsiradiate constrictions per whorl, bounded aperturally by a thickened rib.

The sutures are undecipherable.

Discussion

Relative proportions, expansion rate, position and form of constrictions indicate these specimens to be *Protetragonites*, most closely resembling the well-known species *Protetragonites aeolus* (d'Orbigny). Wiedmann (1962: 23) recognized three subspecies, *P. aeolus aeolus*, *P. aeolus neptuni* Wiedmann (1962: 29, pl. 1 (fig. 2), text-fig. 7b), and *P. aeolus aeoliformis* (P. Fallot) (Wiedmann 1962: 26, pl. 1 (fig. 1), pl. 2 (fig. 4), text-fig. 4a). *P. aeolus aeoliformis* has a more or less rounded whorl section rather than reniform as in the nominate subspecies, whilst *P. aeolus neptuni* has strongly ornamented inner whorls and much more prominent constrictions.

Of other species, *Protetragonites crebrisulcatus* (Uhlig) (Wiedmann 1962: 19, pl. 1 (fig. 3), pl. 3 (figs 2, 4)) has rather similar overall proportions, but bears more constrictions which efface at maturity. *P. obliquestrangulatus* (Kilian) and its subspecies (Wiedmann 1926: 21 *et seq.*) bear many more prorsiradiate constrictions, whilst *Protetragonites laevis* Wiedmann (1962: 31, pl. 10 (fig. 4) text-figs 9–10) has a subquadrate depressed whorl section and is smooth.

Occurrence

Protetragonites aeolus and its subspecies are best known from the western Mediterranean, i.e. the Balearics, Sardinia and south-eastern France, but there are also records from Madagascar, and now Zululand. The species is restricted to the Albian.

SYSTEMATIC POSITION UNCERTAIN

Genus *Pictetia* Uhlig, 1883

Type species

Crioceras astierianus d'Orbigny, 1842.

Diagnosis

Loosely coiled with whorls separated throughout; body chamber may straighten. Whorl section rounded, compressed to depressed; ornamented by weak, irregular, feebly crinkled ribs.

Discussion

Pictetia is an enigmatic genus, known chiefly from septate fragments only which are either curved or straight. Few good illustrations of the type species are available and in consequence the authors reillustrated (Fig. 49) the original of D'Orbigny (1842: pl. 115 (figs 3–5)) which is herein designated lectotype of *P. astieriana* (the specimen has been commonly referred to as the holotype, but D'Orbigny clearly states that he was aware of specimens in the Astier, Duval and Puzos collections, although that which he figured was 'a lévé tous mes doutes a été découverte par M. Astier'. The authors also take the opportunity of illustrating two of the straight fragments, doubtful paralectotypes, also from Escragnolles, Var (Figs 50–51).

In his generic diagnosis of *Pictetia*, Casey (1960: 3) indicated that it had a 'suture line with simple lobe formula I U L E, but highly complex'. Such a formula is not typical of the Lytoceratina, which are characterized by a quinquelobate suture. Unfortunately there is no detailed work on the sutural ontogeny of *Pictetia*; Schindewolf (1961: 678) examined specimens of the type species, and concluded that the small incision in saddle I/U should be regarded as an incision, and not a lobe. If this be true, then *Pictetia* is either to be transferred to the Ancyloceratina (some members of which have fimbriate ornament), as did Schindewolf and Hyatt (1900: 588) before him, or retained within the Lytoceratida as an uncoiled *Lytoceras* (Casey 1960: 3) in which the quadrilobate suture is secondarily derived from quinquelobate ancestors. In *Spiroceras bifurcati* (Quenstedt) Schindewolf (1961: 762, text-fig. 45) demonstrated that two of the original five lobes became so reduced that a pseudo-trilobate condition prevailed in adults; might not reduction in *Pictetia* be a similar reflection of acquisition of the heteromorph habit? Unfortunately the Zululand material does not help in the resolution of this interesting problem.

Occurrence

Pictetia is known from the Lower and Middle Albian of western Europe, Transcaspia, India, Madagascar and Zululand; Collignon (1962*b*: 13) has recorded two species from the Upper Aptian of Madagascar.

Pictetia aff. *depressa* (Pictet & Campiche, 1861)

Figs 52A–C, 53

Compare:

Crioceras depressus Pictet & Campiche, 1861: 28, pl. 45 (figs 3–4).

Pictetia depressa Casey, 1960: 5, pl. 1 (fig. 1a–c), text-fig. 1a–d (with synonomy).

Collignon, 1962*b*: 13, pl. 221 (fig. 457).

Fig. 49. *Pictetia astieriana* (d'Orbigny, 1842). Lectotype, BMNH 46953. × 1.

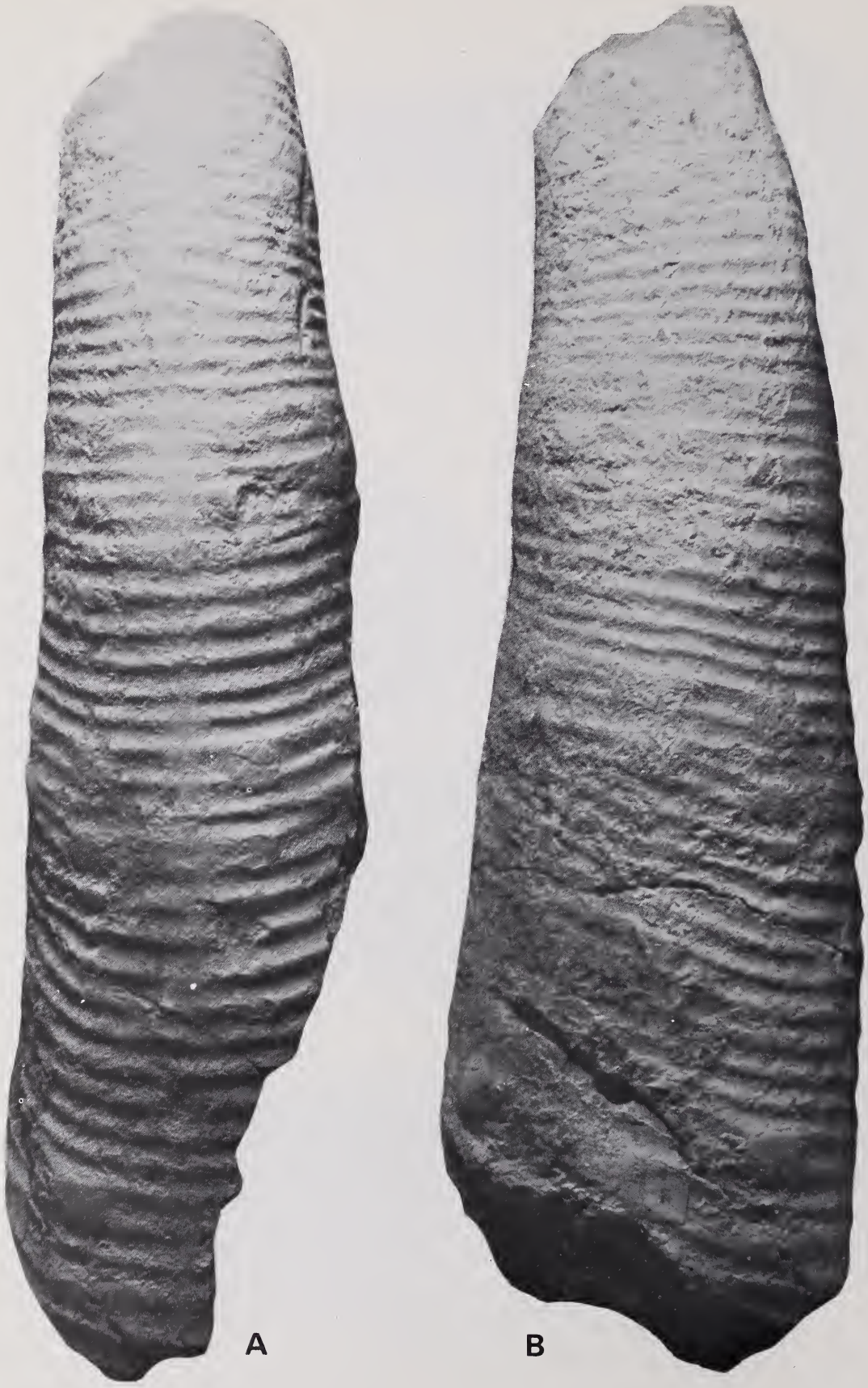

Fig. 50. *Pictetia astieriana* (d'Orbigny, 1842). BMNH C5440, wholly septate ancyloceratid-like shaft. × 1.

Fig. 51. *Pictetia astieriana* (d'Orbigny, 1842). BMNH C5439, septate straight shaft. × 1.

Fig. 52. A–C. *Pictetia* aff. *depressa* (Pictet & Campiche, 1861). SAS LJE 173. × 1. D–F. *Pictetia depressa* (Pictet & Campiche, 1861). Copies of Pictet & Campiche's original figures of the species.

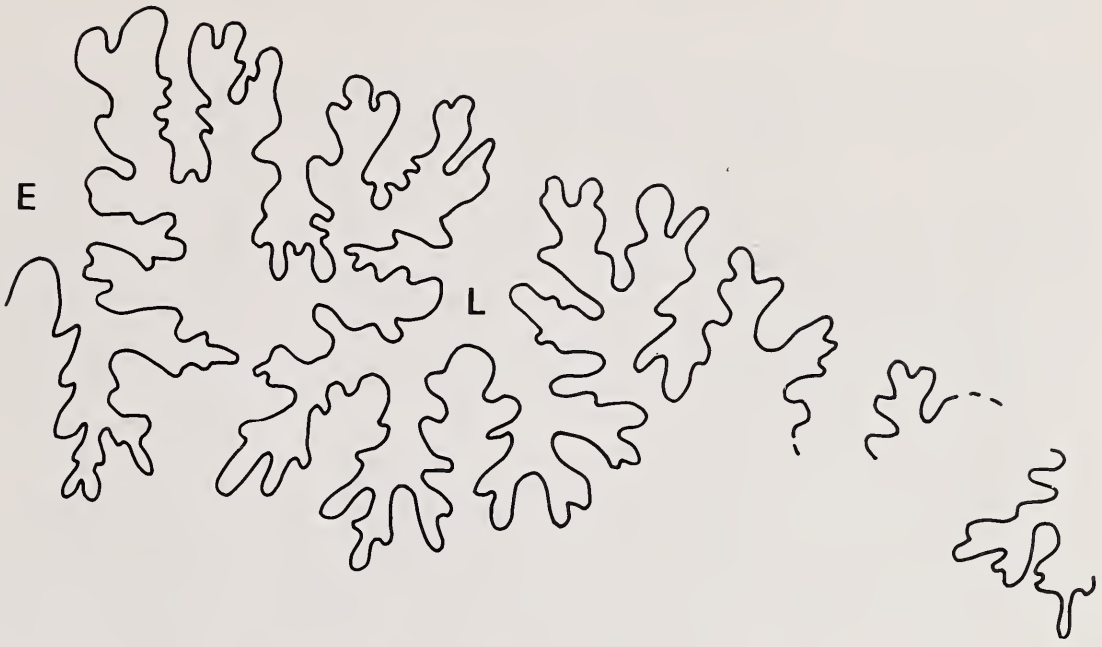

Fig. 53. *Pictetia* aff. *depressa* (Pictet & Campiche, 1861). Suture of SAS LJE 173. × 3,6.

Material

One specimen only, SAS LJE 173 from the Mzinene Formation, Albian II–III, locality 171, Mlambongwenya Spruit, northern Zululand.

Description

The fragment is wholly septate, consisting of three-quarters of a whorl only of a juvenile specimen. Coiling is very open, the whorl section depressed, reniform, with a very small dorsal impressed zone. Ornament is subdued, and consists of single, low prorsiradiate folds on the shell surface. The suture line is partially exposed, showing a long E/L saddle with a narrow stem, a large L and low L/U saddle. I is trifid (Fig. 53).

Discussion

Depressed whorl section, together with the presence of a narrow dorsal impressed area place this specimen closest to Pictet & Campiche's species, the original illustrations of which are reproduced here as Figure 52D–F; the whorl section is more depressed in that species, whilst internal moulds are smooth, in consequence of which the authors refer to their specimen as *P.* aff. *depressa*. In *P. astieriana* (Fig. 49) the whorl section is more rounded; in *P. crassecostata* Collignon (1963: 8, pl. 243 (fig. 1046)) the whorl section is oval with broad, well-differentiated convex ribs; in *P. ovalis* Collignon (1963: 8, pl. 243 (fig. 1045)) the whorl section is also oval, with dense, relatively prominent flexuous ribs. *P. arcuata* Collignon (1962*b*: 13, pl. 221 (fig. 958)) is an Aptian species based on gently curved fragments with a circular whorl section, smooth surface and folds corresponding to the site of individual sutures.

Occurrence

Pictetia depressa is best known from the Lower Albian of western Europe and Transcaspia, although also recorded from the Upper Aptian of Madagascar.

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